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AN ANATOMICAL STUDY OF THE TECTO-PULVINAR PATH IN THE PROSIMIAN *GALAGO SENEGALENSIS*

by

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Department of Psychology
Duke University

Date: October 19, 1978

Approved:

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Irving T. Diamond, Supervisor

William C. Hall

Talmage Peele

Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
Psychology in the Graduate School
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ABSTRACT

(Psychology-Natural Science)

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ABSTRACT

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In primates, the cortex of the temporal lobe expands enormously, and the question arises: Is this cortex sensory, or is it association cortex, as defined in the traditional sense (Diamond, '78; Diamond and Hall, '69)? To answer this question the connections of the tecto-pulvinar path in the prosimian *Galago senegalensis* were studied using the horseradish peroxidase (HRP) and autoradiographic methods for tracing connections (LaVail et al., '73; Cowan et al., '72).

The starting point for this inquiry was the identification of the cytoarchitectonic subdivisions of the occipital and temporal cortex. Following injections of HRP into each individual subdivision, including area 17, but excepting the subdivisions of the auditory cortex, sheets of labeled cells were found in both subdivisions of the pulvinar nucleus organized in some topographic pattern so that, in aggregate, all of the pulvinar projects to all of the visual cortex. Specifically, the entire

pulvinar projects once onto area 17, and at least once onto the extrastriate cortex. The autoradiographic method demonstrates that these intricate arrangements of slab-like zones appear to hold for cortical descending projections as well.

In a second series of experiments, the origins of projection to the pulvinar complex were examined. Regardless of where in the pulvinar complex HRP is injected, labeled cells were always found in the lower half of stratum griseum superficiale of the superior colliculus. In addition, the cortical layers from which descending projections to the pulvinar complex were identified. The results show that layer VI of the extrastriate cortex and V of the striate cortex send descending projections to the pulvinar complex.

In the final series of experiments, HRP was injected into the superior colliculus. The results show, first, that nearly all of the neocortex projects to the superior colliculus and that the projections arise exclusively from layer V. Second, the distribution of labeled cells in the cortex are organized in patterns which correspond to architectonic and functional subdivisions within the cortex and tectum.

From these studies several conclusions seem warranted. First, the entire pulvinar nucleus is the target of the superficial layers of the superior colliculus. Second, the pulvinar complex is interconnected with the entire cortex of the occipital and temporal lobes (excepting the auditory field). The implication of these findings is that the entire cortical

target of the pulvinar complex can be considered primary sensory cortex. Third, all three fields, visual, auditory, and somatic, project to the superior colliculus and each field has a distinct target. The entire visual sensory cortex projects mainly to the superficial layers, while the projections of the auditory and somatic areas are to the deep layers of the superior colliculus. There is one notable exception: The so-called frontal eye fields of the somatic field has descending projections similar to the visual field.

ACKNOWLEDGMENT

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I dedicate this thesis to my parents and my wife, Marcia.

D. R.

CONTENTS

ABSTRACT iii

ACKNOWLEDGMENT vi

LIST OF FIGURES ix

GENERAL INTRODUCTION 1

MATERIALS AND METHODS 5

Horseradish Peroxidase Experiments 5
Autoradiography Experiments 6
Combined Horseradish Peroxidase and Autoradiography Experiments 7
Data Analysis 8

RESULTS 10

I. Organization of Thalamocortical Visual System in *Galago senegalensis* Studied with the Horseradish Peroxidase Method 10

Introduction 10
Experimental Results 12

II. Projections from the Cortex and Brainstem to the Pulvinar Nucleus Studied with the Horseradish Peroxidase Method 64

Introduction 64
Experimental Results 65

III. Projections from the Cortex and Brainstem to the Superior Colliculus as Studied with the Horseradish Peroxidase Method 94

Introduction 94
Experimental Results 96

IV. Projections from the Visual Cortex to the Thalamus and Superior Colliculus Studied with the Autoradiographic Method 124

Introduction 124
Experimental Results 125

DISCUSSION 147

ABBREVIATIONS 180

REFERENCES 184

LIST OF FIGURES

Figure Page

1. Normal cytoarchitecture of the visual cortex, areas 17, 18, and 19. 15
2. Normal cytoarchitecture of the visual cortex, areas temporal posterior and temporal middle. 18
3. Normal cytoarchitecture of the auditory and somatic cortex. 21
4. Experiment 1493L. 25
5. Experiment 1474L. 27
6. Experiment 1372L. 30
7. Experiment 1486R. 32
8. Experiment 1613L. 35
9. Experiment 1504L. 37
10. Experiment 1493R. 39
11. Experiment 1480L. 42
12. Experiment 1486L. 44
13. Photomicrograph of HRP labeled neurons. 46
14. Experiment 1529R. 49
15. Experiment 1611L. 51

Figure Page

16. Experiment 1611R. 53

17. Experiment 970L. 56

18. Experiment 1626L. 59

19. Photomicrograph of HRP injection site. 61

20. Photomicrograph of HRP labeled neurons. 63

21. Experiment 1141R. 67

22. Experiment 1199R. 70

23. Experiment 1143R. 73

24. Experiment 1270R. 76

25. Experiment 1318R. 79

26. Experiment 1315L. 82

27. Experiment 1133R. 85

28. Experiment 1306L. 88

29. Experiment 1397R. 91

30. Experiment 1391L. 93

31. Experiment 1310L. 98

32. Experiment 1571L. 101

33. Experiment 1321L. 104

34. Experiment 1141L. 107

35. Experiment 1293L. 111

36. Experiment 1294L. 114

37. Experiment 1541L. 117

Figure Page

38. Experiment 1128L. 119

39. Experiment 1571R. 123

40. Experiment 1217L. 127

41. Experiment 1474L. 132

42. Experiment 1486R. 134

43. Experiment 1486L. 137

44. Experiment 1507L. 140

45. Experiment 1460R. 144

46. Experiment 1480R. 146

47. Summary diagram of the pulvinar projections to the cortex 153

48. Experiments 1529L and 1495R. 172

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GENERAL INTRODUCTION

In The traditional view ~~of~~ of sensory systems the visual pathway~~s~~ begins with the projections of the optic tract to the lateral geniculate nucleus~~,~~s ~~which then relayed~~ where visual impulses are relayed to the striate cortex~~ of area 17~~. The belt of cortex adjacent to the striate area, areas 18 and 19, was regarded as a visual association or visual psychic area, the function of which was to transform simple visual sensations into the visual perception of objects. Cortico-cortical pathways to the temporal cortex provided a still higher level of integration since the visual perception was related to perceptions based on other modalities (~~see~~ C.f. Campbell '05 for review, see Diamond, '79).

The discovery that the pulvinar nucleus in primates projects to areas 18, 19, and the temporal lobe conflict~~s~~ed with the idea that these areas are association areas in the strict sense (Walker — LeGros Clark). However, the basic idea underlying the traditional view could be preserved by postulating that the pulvinar nucleus receives projections only from other thalamic nuclei ~~from~~ including the sensory relay nuclei [illegible] ~~of the thalamus.~~ The pulvinar nucleus thus became the "association area" of the thalamus (Rose and Woolsey, '49b).

We began our inquiry into the ~~evolution of the~~ visual cortex with the idea that the evolution of the pulvinar nucleus and its connections holds the key to the nature of the so-called association cortex of the occipital and temporal lobe. In the

initial experiments, a nucleus in the posterior thalamus of the tree shrew was identified as the precursor of the pulvinar nucleus in primates (Snyder and Diamond, '68; Killackey et al., '71). It was then found that this homologue of the pulvinar nucleus was in fact a visual sensory nucleus relaying visual impulses from the superficial layers of the superior colliculus to the temporal lobe and to areas 18 and 19 (Diamond et al., '70; Harting et al., '73a, b).

The next question was to find out whether the pulvinar nucleus in a prosimian primate received fibers from the superficial layers of the superior colliculus. Experiments using the method of anterograde degeneration showed that only a part of the pulvinar nucleus in the Galago received fibers from the superior colliculus. ~~and in turn this~~ Further experiments using both anterograde & retrograde degeneration ~~showed~~ suggested ~~tecto-recipient zone projected~~ that the tecto recepient zone of the pulvinar nucleus projected only to a part of the temporal lobe, area Tm ~~(Glendenning et al., '75).~~ ~~STOP~~ Stop.

The advent of the recent transport methods provides a new opportunity to continue the inquiry of the tecto-pulvinar path in Galago. The starting point of this ~~inquiry~~ ~~paper~~ report is the identification of the cytoarchitectonic subdivisions of the Galago cortex. The chief features of the major fields provide the basis of the first part of section I. The key to understanding the significance of the cortex, and especially the cytoarchitectonic subdivisions of the cortex, lies in the study of the afferent projections to the cortex and the efferent projections from the cortex. This proposition has been the first principle of the study of the cortex since the days of

Elliot Smith ('10). Guided by this principle, horseradish peroxidase (HRP) was injected into each of the various subdivisions of the temporal and occipital cortex to study ascending projections, and the patterns of labeled cells in the dorsal lateral geniculate body and the pulvinar nuclei were charted. The results of these experiments are contained in the second part of section I.

The study of descending projections also provides clues for understanding the significance of the tecto-pulvinar path. To examine the cortical descending projections to the pulvinar complex and superior colliculus, two strategies were employed. The first approach utilized the retrograde transport of HRP to reveal the total area of cortex which projects descending fibers to small portions of the pulvinar and tectum. The second approach made use of the anterograde transport of tritiated amino acids to reveal the entire target of one small area of cortex. In other words, the retrograde method complements the anterograde method, each technique capable of revealing some feature of a pathway beyond the capabilities of the other. The results of these experiments from the basis for the remaining result sections. In the second section the projections to the pulvinar nucleus form the tectum and the cortex, as revealed by the retrograde transport of HRP, are presented. In the third section, the results of experiments in which HRP is injected into the superior colliculus are described. Finally, the results of injecting tritiated amino acids into the various subdivisions of the striate and

extrastriate cortex are presented in section IV.

As a result of these experiments, the connections of the tecto-pulvinar system have taken on a new significance. First, the entire pulvinar nucleus is the target of the superficial layers of the superior colliculus. Second, the pulvinar complex is interconnected with the entire cortex of the occipital and temporal lobes (excepting the auditory field). The implication of these findings is that the entire target of the pulvinar complex can be considered primary sensory cortex. Third, all sensory cortex projects to the superior colliculus and each field has a distinct target: The entire visual sensory cortex projects mainly to the superficial layers, while the projections of the non-visual cortices are to the deep layers of the tectum.

MATERIALS AND METHODS

A total of 70 Galago senegalensis were used in this study. The methods used involved the retrograde axonal transport of HRP and the anterograde axonal transport of tritiated amino acids.

In preparation for each experiment, the animal was anesthetized with ketamine hydrochloride (50 mg/kg). For visually guided cortical injections the animal was secured in a non-traumatic holder which enabled the head to be oriented in a variety of planes (Erickson, '66). For subcortical placement of injections, a stereotaxic instrument was utilized.

Horseradish Peroxidase Experiments

Nearly all of thalamic and tectal injections and some of the cortical injections were made with an electrophoretic delivery system (see Graybiel and Devor, '74). Glass micropipettes, with tip bevels ranging from 30-70 um (inside diameter) were secured to the stereotaxic carrier and were filled with a 30% solution of HRP (Sigma, type VI, or Boehringer, grade I) dissolved in Tris buffer at pH 7.6. A steel wire placed in the shank of the pipette served as the conductor between the power source (SD-5 Grass stimulator) and the solution. For injection, DC

current (delivered in 2 square wave pulses per second) was applied between the pipette lead and exposed muscle. A continuously monitored current of 1-2 uA was applied for 45 minutes. In the remaining experiments, pressure injections of HRP were made with a 1 ul Hamilton syringe fitted with a beveled glass pipette with an inside diameter of 60 um. In these experiments 0.05-0.1 ul of HRP was injected over a 30-minute period.

After survival periods of 24-48 hours, the animals were perfused with a mixture of 0.5% paraformaldehyde and 2.5% glutaraldehyde in 0.1 M sodium cacodylate or phosphate buffer. The brain was blocked and immersed in a 30% sucrose buffer solution at 4° C until it sank. Frozen sections (40-60 um) were cut and processed for HRP histochemistry. Some of the brains were incubated in a bath containing a 0.5% solution of 3, 3'-diaminobenzidine tetrahydrochloride and 0.01% hydrogen peroxide (LaVail et al., '73). The other brains were reacted in a bath containing a 0.5% solution of benzidine dihydrochloride and 0.01% hydrogen peroxide (Mesulam, '76). The incubated sections were then washed, mounted on previously prepared gel-coated slides and air dried. The tissue was then lightly stained with cresyl violet acetate or neutral red.

Autoradiography Experiments

One experiment was done on each hemisphere of 14 *Galago senegalensis*. Single injections of an equal parts mixture of tritiated

leucine and proline, evaporated under nitrogen and redissolved in sterile saline to a concentration of 50 uCi/ul, were made into individual cortical subdivisions. Injections were made through glass micropipettes with inside diameter tip bevels of 40-60 um cemented over the needle of a 1 ul Hamilton syringe.

After survival periods of 1-4 days, the animals were perfused with 10% formalin. The brain was blocked, removed from the skull, and allowed to sink in a sugar formalin solution at room temperature. Frozen sections (40 um thick) were cut, mounted on previously prepared gel-coated slides, air dried overnight, and defatted with ethyl alcohol and xylene. The tissue was then coated with Kodak NTB-2 emulsion diluted 1:1 with water and stored for 2-8 weeks at 4° C. The exposed slides were developed in Kodak D-19 at 15° C, fixed and stained through the emulsion with cresyl violet acetate (Cowan et al., '72; Edwards, '72).

Combined Horseradish Peroxidase and Autoradiography Experiments

Some animals received injections of both HRP and tritiated amino acids. The procedures for preparing each tracer was identical to that described above. The injection device was a 1 ul Hamilton syringe fitted with a beveled glass micropipette. Each solution was injected separately in an attempt to equalize the injection area of the two tracers. Following a 1-2 day survival, the animal was perfused with a mixture of 0.5% paraformaldehyde and 2.5% glutaraldehyde in 0.1 M phosphate buffer.

The brain was allowed to sink in a sugar buffer solution, and after cutting 40 um sections, half of the sections were reacted for HRP histochemistry and the other half were prepared for autoradiography.

Data Analysis

For identifying the distribution and location of labeled HRP neurons and reduced silver grains, both bright and dark field condensors were used. Data from individual brain sections were transferred, with the aid of an X-Y plotter coupled to the microscope stage or with a drawing tube attachment, onto outline drawings of the individual sections magnified 15 or 20 times. This resulted in a drawing of the position of the HRP labeled neurons or the distribution of autoradiograph label relative to the borders of the section or other outstanding landmarks, but without regard to cytoarchitectonic subdivisions. Next, these sections were drawn with the aid of a microprojector and microscope to establish cytoarchitectonic boundaries without regard to the locus of the HRP neurons or the autoradiograph label. Finally, the two drawings were superimposed to make a final chart, and the HRP labeled cells and the distribution of autoradiographic label were examined under the microscope to verify their positions relative to the subdivisions of the thalamus and brainstem indicated in the final figures.

To show the site of the cortical injection, the surface of the brain was reconstructed and the injection site was projected onto a lateral

view of the cortex. A careful study of the cytoarchitectonic characteristics of the cortex injected was made to verify the final position of the injection site on the reconstruction.

RESULTS

I. Organization of Thalamocortical Visual System in Galago senegalensis Studied with the Horseradish Peroxidase Method

Introduction

The cortical projections of the pulvinar complex of Galago senegalensis have been previously studied first with retrograde degeneration and later with anterograde degeneration techniques. In the retrograde studies (Atencio et al., '75; M. Wilson, experiments in progress), the absence of severe degeneration after small restricted cortical lesions prevented arriving at a picture of the precise projection targets of each small area of the pulvinar complex. In general it was found that lesions of area Tm produced a band of slight to moderately severe degeneration in the inferior pulvinar nucleus. Cortical lesions ventral to area Tm always led to moderate or severe degeneration in the region of the thalamus lying between the inferior pulvinar nucleus and the posterior group, an area designated a transition zone. Removal of the cortex intercalated between area Tm and the striate area resulted in severe degeneration in the superior pulvinar, while lesions of areas 17 and 18 led to retrograde changes at the border between the inferior and superior divisions of the pulvinar nucleus.

The anterograde degeneration studies were guided by the discovery that the superficial layers of the superior colliculus projected only to the caudal half of the inferior pulvinar nucleus (Glendenning et al., '75; Harting et al., '72). Lesions restricted to this tecto-recipient zone were achieved in several experiments with the result that cortical degeneration appeared in two discrete patches in the temporal lobe, one zone in area Tm and a second zone in the cortex ventral to area Tm. However, it seemed reasonable at the time to attribute the ventral patch to the interruption of fibers. In this way, the tecto-recipient pulvinar could be given a single target in the cortex, leaving the rostral half of the inferior subdivision along with the transition zone to project to the cortex below area Tm (Glendenning et al., '75).

Lesions involving the superior pulvinar usually produced two or more zones of degeneration, one in areas 18 and 19 and a second in the cortex below area Tm. No projection from the pulvinar complex to area 17 was revealed by either degeneration method (Glendenning et al., '75).

But in spite of intensive efforts using both retrograde and anterograde degeneration methods, a complete understanding of the relationships between the pulvinar complex and its cortical projection field has not been achieved. To advance this inquiry, we have attempted to define the total projection field of the pulvinar nucleus using the retrograde transport of horseradish peroxidase (HRP). To achieve this aim, it was necessary first to subdivide the posterior neocortex into its cyto-

architectonic areas. The results will demonstrate a different pattern of projection from the thalamus to each distinct subdivision of the posterior neocortex. After every injection, labeled cells were always found in both subdivisions of the pulvinar nucleus, organized in some topographic manner, so that, in aggregate, the entire pulvinar nucleus projects to all of the posterior neocortex. Specifically, the results indicate that both the striate and extrastriate cortex are targets of the entire pulvinar complex.

Experimental Results

Part 1: The Subdivisions of the Neocortex in Galago

The experimental results now to be presented will define the total projection field of the pulvinar nucleus. We will argue that this entire cortical field can be equated to primary visual cortex since every part of the pulvinar nucleus receives projections from the superficial layers of the superior colliculus as well as from the striate cortex. The results will also provide a basis for analyzing the organization of these projections, but to achieve this aim it was necessary first to subdivide the posterior neocortex into its cytoarchitectonic areas. We will show that each of these areas receives projections from the pulvinar nucleus and further that the pattern of the distribution of labeled cells is different for each subdivision.

The striate cortex of Galago has been described before (Glendenning

et al., '76), and here it is only necessary to point out those features which stand in marked contrast to every other area of the visual field (see figure 1). First, only in the striate cortex is layer IV the darkest layer. In turn, layer IV is subdivided into two tiers, a superficial lighter sublayer which receives projections from the magnocellular layers 1 and 2 of dorsal lateral geniculate body and a deeper and darker sublayer. At the border between areas 17 and 18 all of the distinguishing features of area 17 end abruptly (see figure 1). Layer IV remains distinct but is now light. Layer III is darker and the deep pyramidal cells of this layer are conspicuously larger and more deeply stained. Layer V is also darker although the largest pyramids in area 18 are not as large or deeply stained as the solitary cells of Meynert in area 17.

It is conventional to divide the belt adjacent to the striate cortex into two strips, areas 18 and 19, although in Galago at least there is no sharp border between them. In our experience the most reliable way to identify area 18 in contrast to 19 is to find large pyramidal cells at the base of layer III. Area 19 can also be distinguished from area 18 in the position of the large pyramidal cells of layer V. Those large cells of area 19 are more likely to encroach on layer IV. It is, of course, conventional to speak of areas 18 and 19 as "occipital lobe" as distinguished from the "temporal areas" we will now describe. We do not wish to make an issue of this traditional terminology as long as it is clearly understood that there is no connectional or architectonic basis for it.

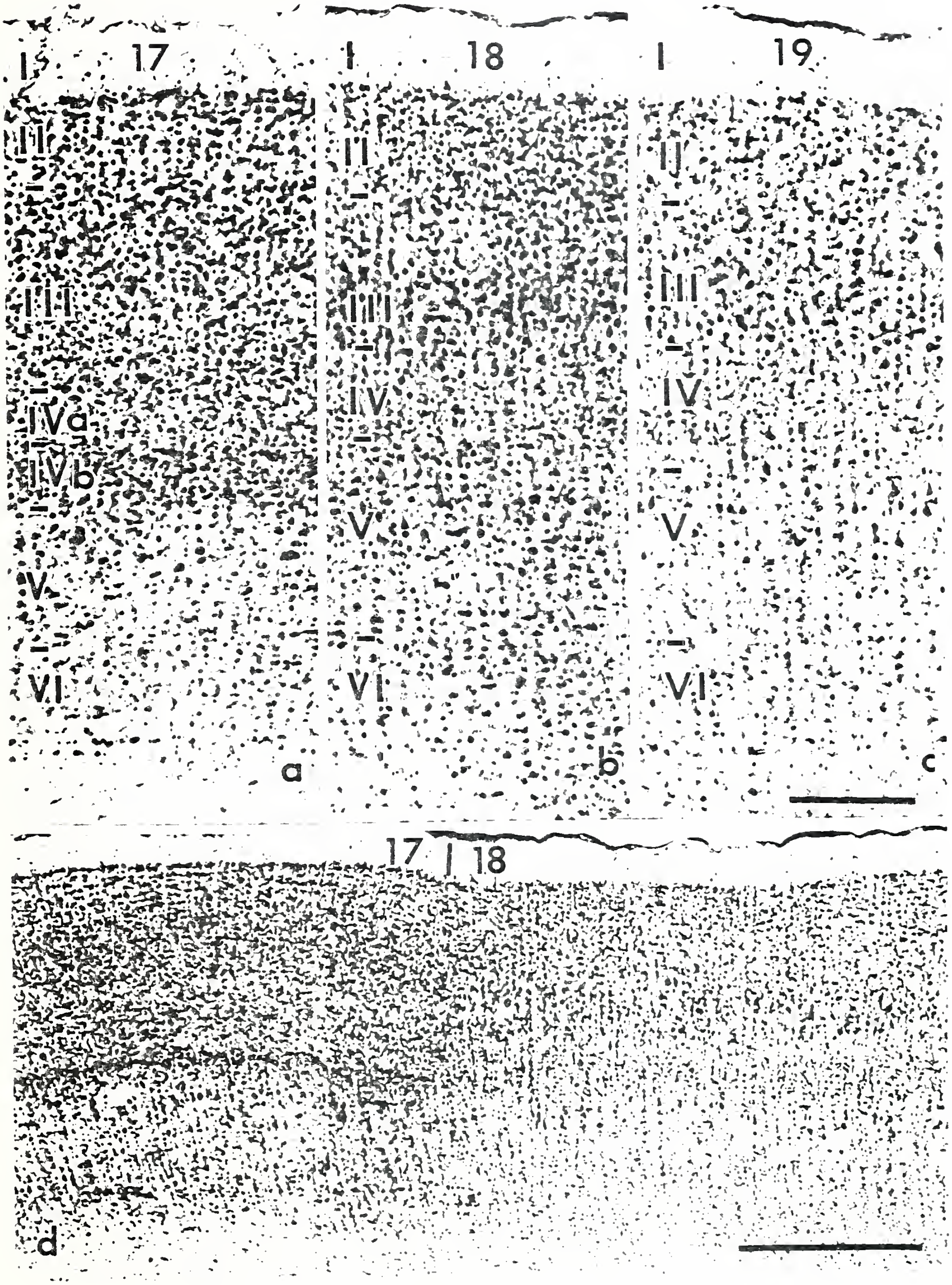
Figure 1. Photomicrographs to show the features of the visual field. Celloidin embedding; 50 um section. Bar, .5mm.

a. a section through area 17 illustrating the split IVth layer and the light layer V.

b. a section through area 18 illustrating layer III and the deep pyramidal cells in this layer.

c. a section through area 19 illustrating the large pyramidal cells in layer V encroaching on layer IV.

d. a section to show the 17-18 border.


I
17
II
III
IVa
IVb
V
VI
a
I
18
II
III
IV
V
VI
b
I
19
II
III
IV
V
VI
c
17
18
d

There is no more reason for separating area 19 from the areas lying in front of it than there is for separating the divisions we will now describe. The important border lies not between area 19 and the temporal areas but between the auditory and visual fields as we will try to defend later.

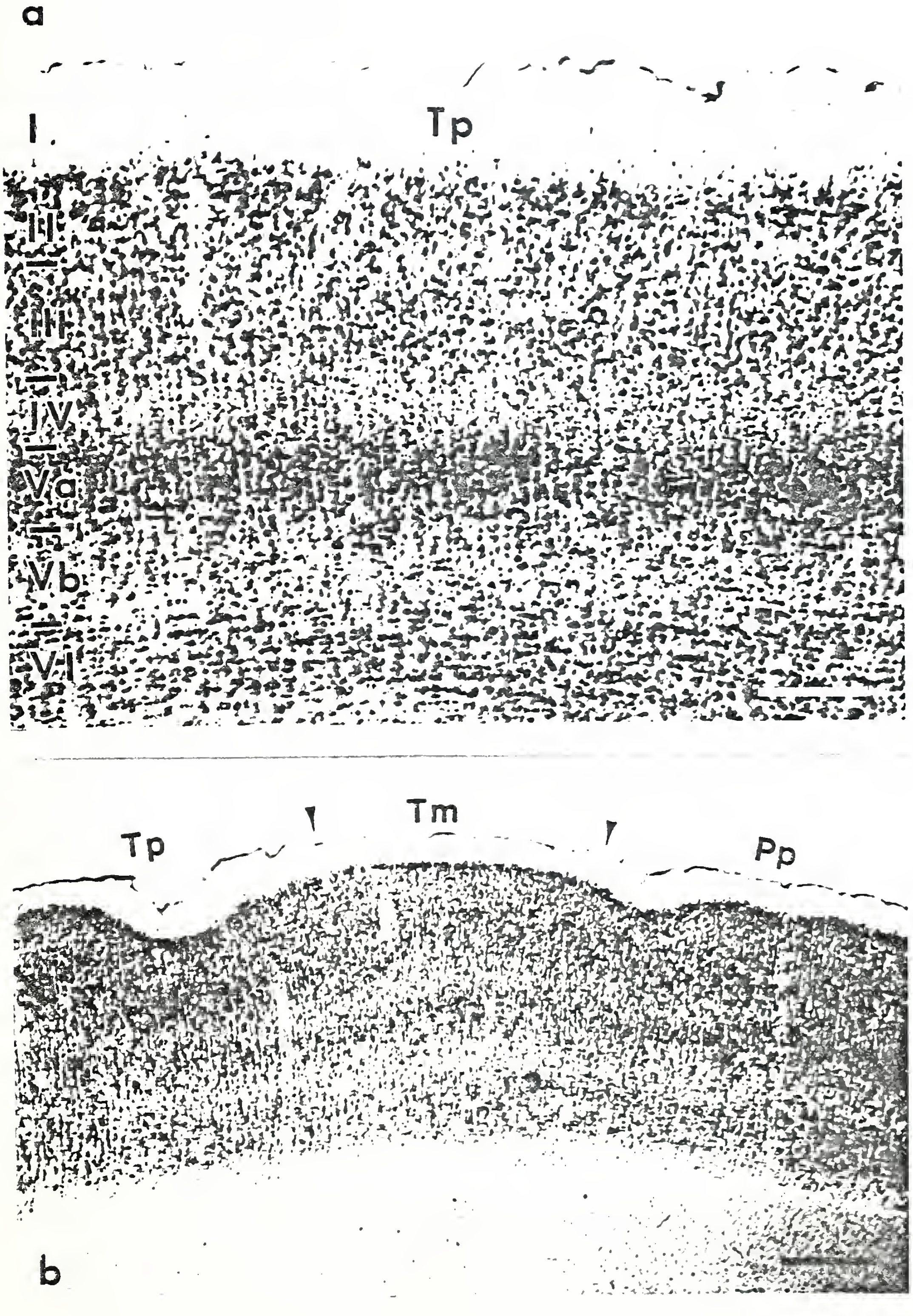
It is best to begin the description of the visual temporal areas with a subdivision we call "Temporal posterior" because all of the areas adjacent to Tp appear to be variations on the pattern shown by Tp. The hallmark of area Tp is the split layer V. The upper tier of layer V is dark with the dense population of medium-sized pyramids. The lower tier of layer V is very light, being sparsely populated with dark pyramids and containing a number of small, lightly staining cells. Since layer IV is also very light, layer Va stands out as a conspicuous dark band much as layer IV stands out in the striate cortex (see figure 2a).

All of the surrounding areas resemble Tp. Tm is the most distinctive. The even or straight borders between layers III, IV, and Va which characterize area Tp are conspicuously absent in Tm. In Tm layer IV is much wider and its small cells penetrate layer III (see figure 2). The areas lying ventral and rostral to Tp can be considered as large transition zones which closely resemble Tp. For example, in Tv the features which characterize Tp gradually disappear around the ventral surface from Tp to the proisocortex or to area 18 on the medial wall. The ventral borders of Ta and Tv are, in contrast, quite sharp. For example, the auditory field rostral to area Ta is usually marked by a

Figure 2. Photomicrographs to show the features of the temporal cortex. Celloidin embedding; 50 um section. Bar, .5 mm.

a. a section through the posterior temporal area illustrating the split layer V.

b. a section to show the features of the posterior temporal area, at the left, and the middle temporal area on the right. Note that the even borders between layers III, IV, and Va which characterize the posterior temporal area are absent in the middle temporal area.


a
I
Tp
II
III
IV
Va
Vb
VI
Tp
Tm
Pp
b

dimple or small sulcus on the other side of which lies the posterior auditory area which we believe to be the homologue of the posterior ectosylvian gyrus of the cat.

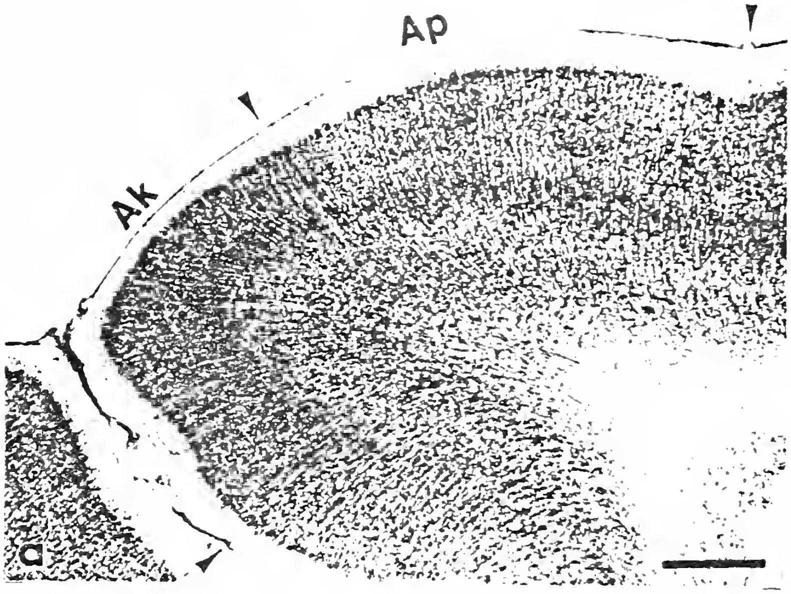
A word about the posterior parietal area is necessary. Once again the term "parietal" is based on tradition and does not reflect any evidence about connections. In fact, our evidence about the projections to the posterior parietal area remains incomplete. There is a suggestion that a part of this area actually belongs to the visual field, that is, to the projection field of the pulvinar nucleus. Cytoarchitectonically, the posterior parietal cortex is characterized by the very dark appearance of the upper tier of layer V.

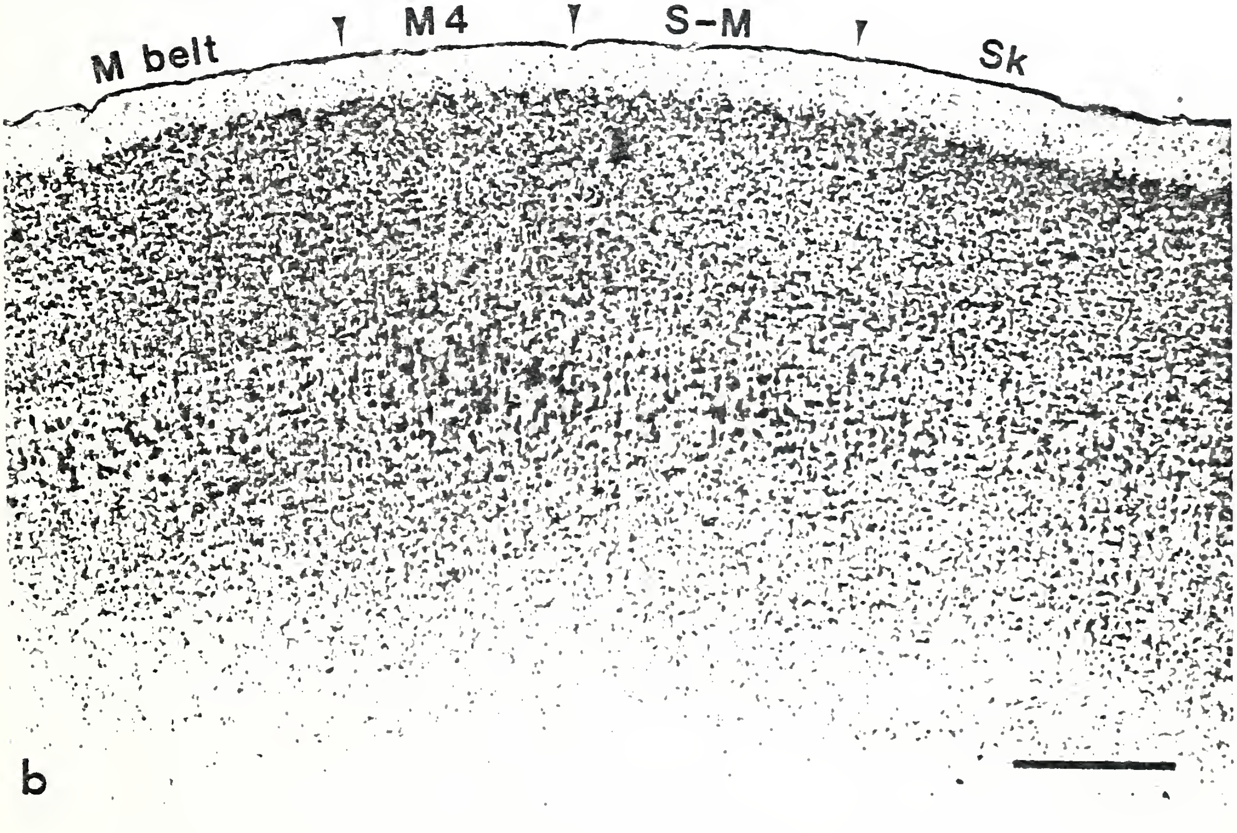
At this point, it is convenient to present our description of the auditory and somatic cortical fields. This particular account is especially related to the experiments in which HRP is injected into the superior colliculus (see Results, III). The auditory koniocortex lies at the rostral pole of the temporal lobe and is characterized by a fusion of layers II, III, and IV (see figure 3). Thus, the auditory primary area is very different from the striate cortex where there is little or no mixing of granular cells with the pyramidal cells of layer III. Layer V is broad and light and layer VI is also light in comparison with the areas of the occipital lobe. The belt around AI or the primary auditory cortex is similar to AI in the fusion of layers III and IV, but these superficial layers are not as densely populated while layer V is more densely

Figure 3. Photomicrographs to show the features of the auditory and somatic fields. Celloidin embedding; 50 um section. Bar, .5 mm.

a. a section through the auditory field. The auditory koniocortex at the rostral pole of the temporal lobe is characterized by a fusion of layers II, III, and IV.

b. a section through the somatic field illustrating a common broad layer V containing huge pyramidal cells at varying depths. Motor 4 is dysgranular while somatic koniocortex is characterized by a dense population of small cells in the superficial layers.


Ap
Ak
a


M belt
M4
S–M
Sk
b

populated and the pyramidal cells of the deeper layers are larger and more deeply stained. Between the auditory belt and the temporal area Ta is a broad band where layer IV separates from layer III and layer V splits. This band is intermediate between the primary auditory area and the temporal areas in cytoarchitecture, but the evidence from connections shows it is part of the auditory belt and specifically that it is homologous to the posterior ectosylvian gyrus of the cat (Fitzpatrick et al., '77).

All of the subdivisions of the somatic field share in common a broad layer V containing huge pyramidal cells at varying depths (see figure 3). In other words, layer V is not split as it is in the temporal lobe. The pyramids are largest in the Motor area (area 4 using Brodmann's terminology) and smallest in the koniocortex. Motor 4 is, of course, dysgranular, while somatic koniocortex is characterized by a dense population of small cells in the superficial layers. Between somatic koniocortex and somatic motor 4 is a band which appears intermediate between the dysgranular and highly granular regions. This transition zone is labeled "sensory-motor" in figure 3. Again, all three zones have much in common, notably the irregular distribution of large pyramids in layer V.

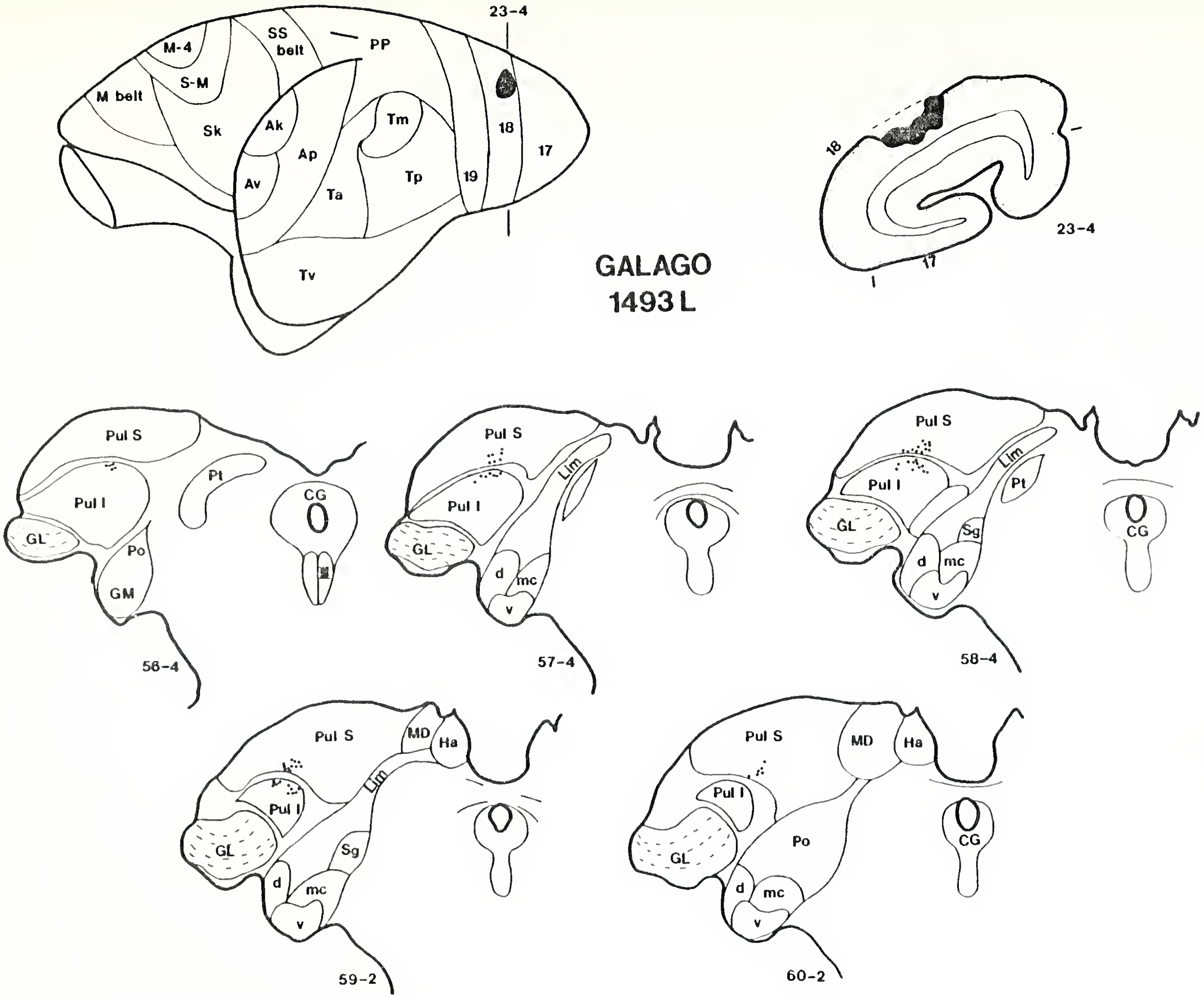
Part 2: HRP Injections in the Cortex

Injections of area 18. The two experiments with injections into area 18 not only reveal a pattern of distribution of labeled cells in the pulvinar complex but also provide a chance to test the method of

assessing the cortical region incorporating HRP. If we seem to belabor this point it is because the method is still relatively new, and if the area incorporating HRP is underestimated the results cannot be interpreted in a meaningful way. Figure 4 shows that in experiment 1493L the HRP diffused just to the border of area 17 but did not cross it. No labeled cells were found in the dorsal lateral geniculate body. In contrast, the injection of HRP in case 1474L (see figure 5) just crossed the border of area 17 and, as a result, a few labeled cells were seen in the caudal sector of the dorsal lateral geniculate body. The number of labeled cells in the dorsal lateral geniculate body is only a small fraction of the number seen when the injection is centered in area 17.

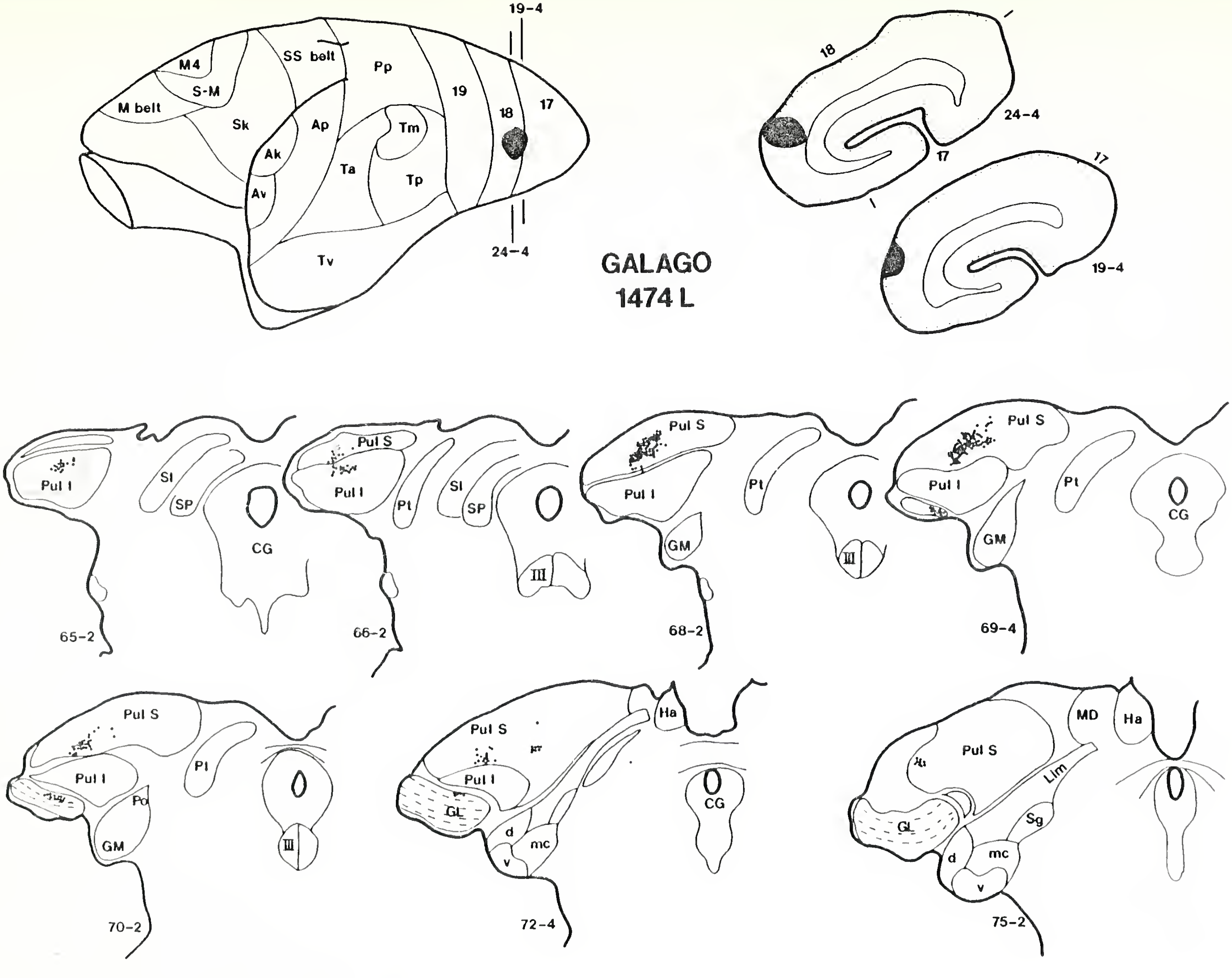
Both experiments show the same pattern of labeled cells in the pulvinar nucleus. The cells are centered in the very middle of the pulvinar nucleus on the border between the superior and inferior divisions and are distributed in the form of curved sheets, one limb of which arcs into the superior division and one limb of which remains in the inferior pulvinar nucleus. Since both injections almost certainly involved the zero vertical meridian on the 17-18 border, it is fair to conclude that the distribution of labeled cells included the representation of the zero vertical meridian in the pulvinar complex. More specifically, it is likely that the zero vertical meridian is represented in parallel lines adjacent to the fiber band that divides the pulvinar nucleus into two main divisions.

Figure 4. To show the distribution of labeled neurons in the thalamus after an injection of HRP into area 18 in *Galago* 1493L. The following conventions appl~~ies~~y to the next 14 line drawings. The locus of the injection is depicted in black on a lateral view of the cortex, and on the frontal section through the injection site. Each black dot within the thalamus represents a single labeled neuron. Abbreviations for this and succeeding figures appears on page



GALAGO
1493 L

Figure 5. To show the distribution of labeled neurons in the thalamus after an injection of HRP into area 18 in Galago 1474L.



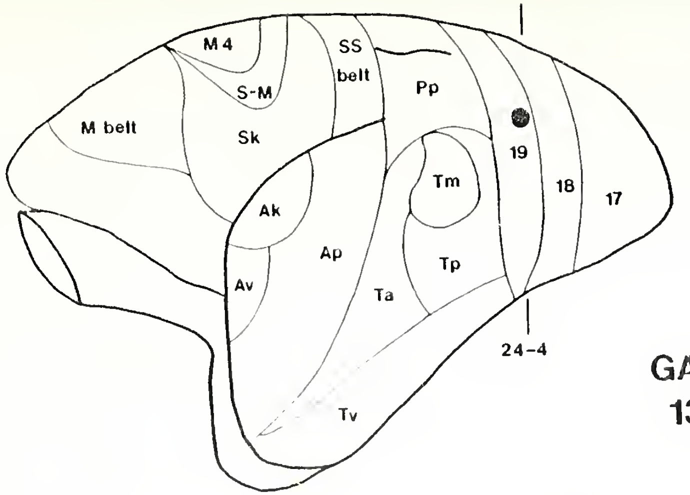
GALAGO
1474 L

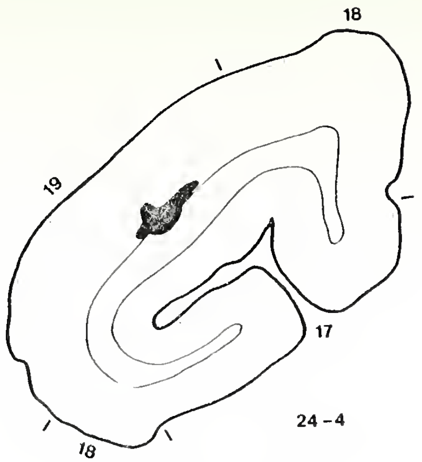
A case to show the effect of injecting HRP into the underlying white matter. Out of 23 experiments only in one case did the HRP appear to enter transected fibers. That experiment (Galago 1372L) is illustrated in figure 6. The results show first that there are widely scattered labeled cells in the dorsal lateral geniculate body and both major subdivisions of the pulvinar nucleus. This distribution does not fall into any of the recognizable patterns to be described next, and it is the only case where an injection of the extrastriate cortex stained cells of the lateral geniculate body.

Injections of area 19. There are four cases of injections into 19 and the pattern of labeled cells in each case was similar. Figure 7 shows the results of experiment 1486R which can be taken as representing the group. First, the labeled cells are mainly in the superior pulvinar, extending into the rostral extremity of that division. Second, the labeled cells are concentrated in two separate loci at some levels (see, for example, section 52-2), but after viewing the entire distribution of labeled cells there is little doubt that the cells constitute one continuous sheet which begins in the ventral lateral core of the superior pulvinar division, extends up along its lateral margin and then turns medially and curves around and down to form a half circle (see section 53-4). Third, there are a few cells in the inferior pulvinar nucleus and these constitute the very caudal extremity of the curved sheet. If the injection is lower in 19, there are many more cells in the inferior pulvinar nucleus. In

Figure 6. To show the distribution of labeled neurons in the thalamus after an injection of HRP involving the underlying white matter in *Galago* 1372L.

GALAGO
1372 L





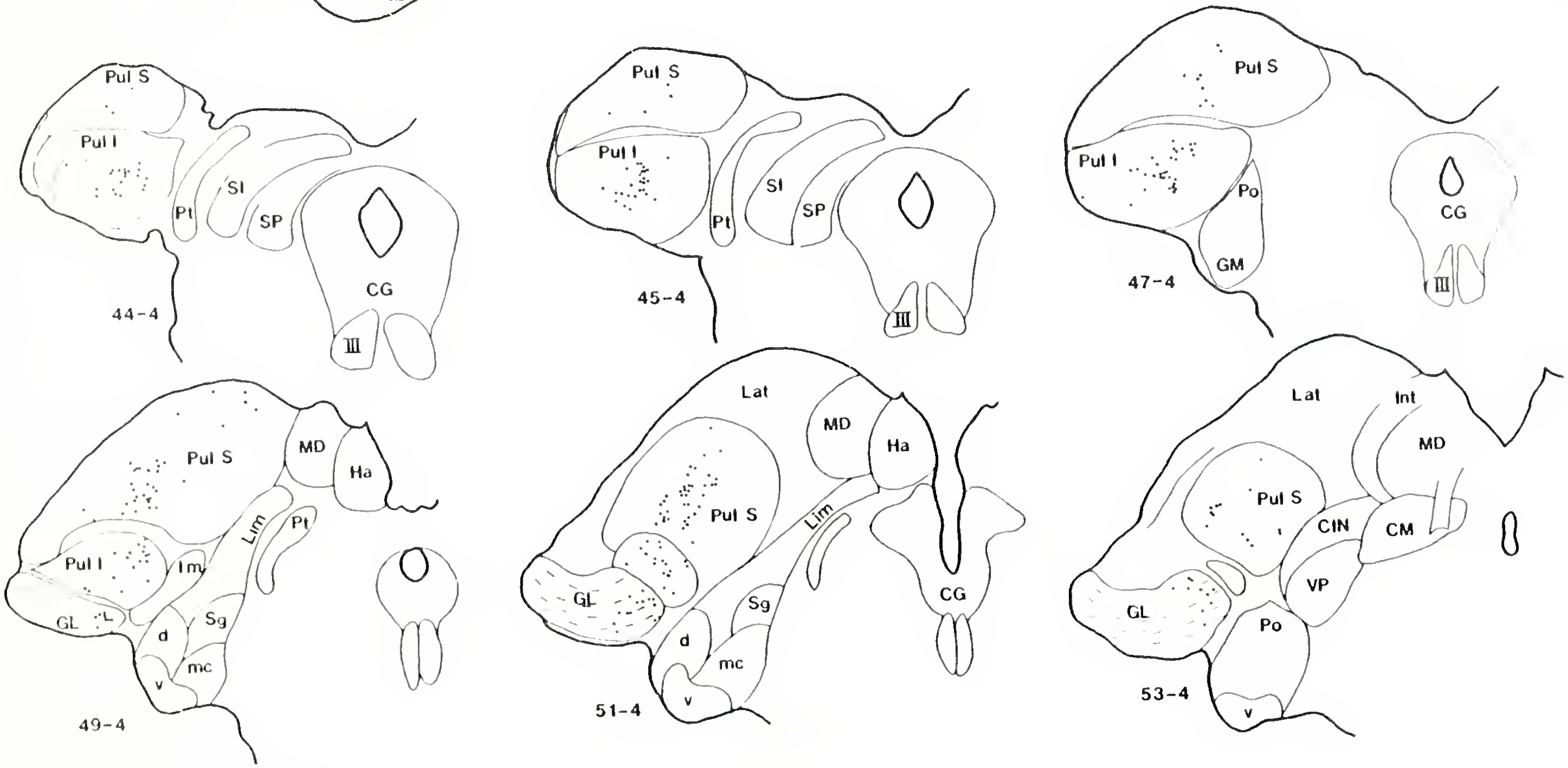
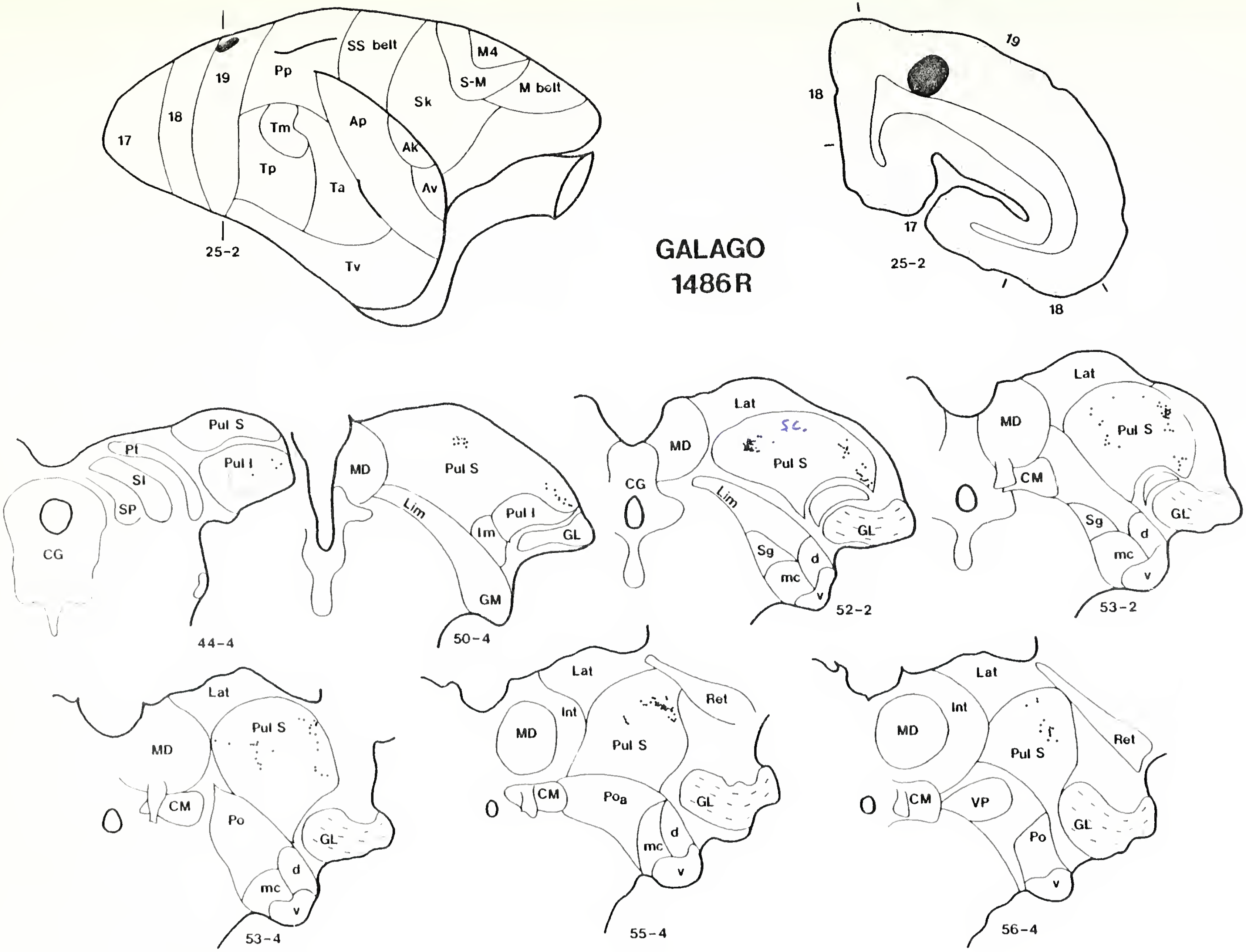


Figure 7. To show the distribution of labeled neurons in the thalamus after an injection of HRP into area 19 in Galago 1486R.


GALAGO
1486R

one of the four cases, the HRP entered the posterior parietal area with essentially the same result, which is to say all labeled cells were in the pulvinar nucleus and most of these were in the rostral part of the superior division. This is our evidence, admittedly not convincing by itself, that the pulvinar nucleus also projects to a part of the posterior parietal area, at least that part lying just above area Tm.

Injections of the middle temporal area (Tm). There were four injections into area Tm and all of them led to a heavy concentration of labeled cells in the rostral part of the inferior division. The similarity in the distributions can be seen by comparing cases 1613L and 1504L (see figures 8 and 9). There are two important points to make about this pattern. First, the column in the inferior pulvinar nucleus does not include all of the cells; as the column is followed rostrally, it moves dorsally and medially, extending into the superior pulvinar nucleus. Second, the locus of the greatest concentration of labeled cells is along the ventral border of the inferior pulvinar nucleus. Since, on the basis of the area 18 injections, the representation of the zero vertical meridian has been placed along the common border formed by the two major subdivisions of the pulvinar complex, the distribution of labeled cells in these two experiments lies outside this representation.

The results of case 1493R (see figure 10) are similar to the other two cases in that the focus of concentration is in the rostral part of the inferior pulvinar division but differs in that the column or sheet is more

Figure 4. To show the distribution of labeled neurons in the thalamus after an injection of HRP into area 18 in Galago 1493L. The following convention applies to the next 14 line drawings. The locus of the injection is depicted in black on a lateral view of the cortex, and the frontal section through the injection site. Each black dot within the thalamus represents a single labeled neuron. Abbreviations for this and succeeding figures appears on page 180.

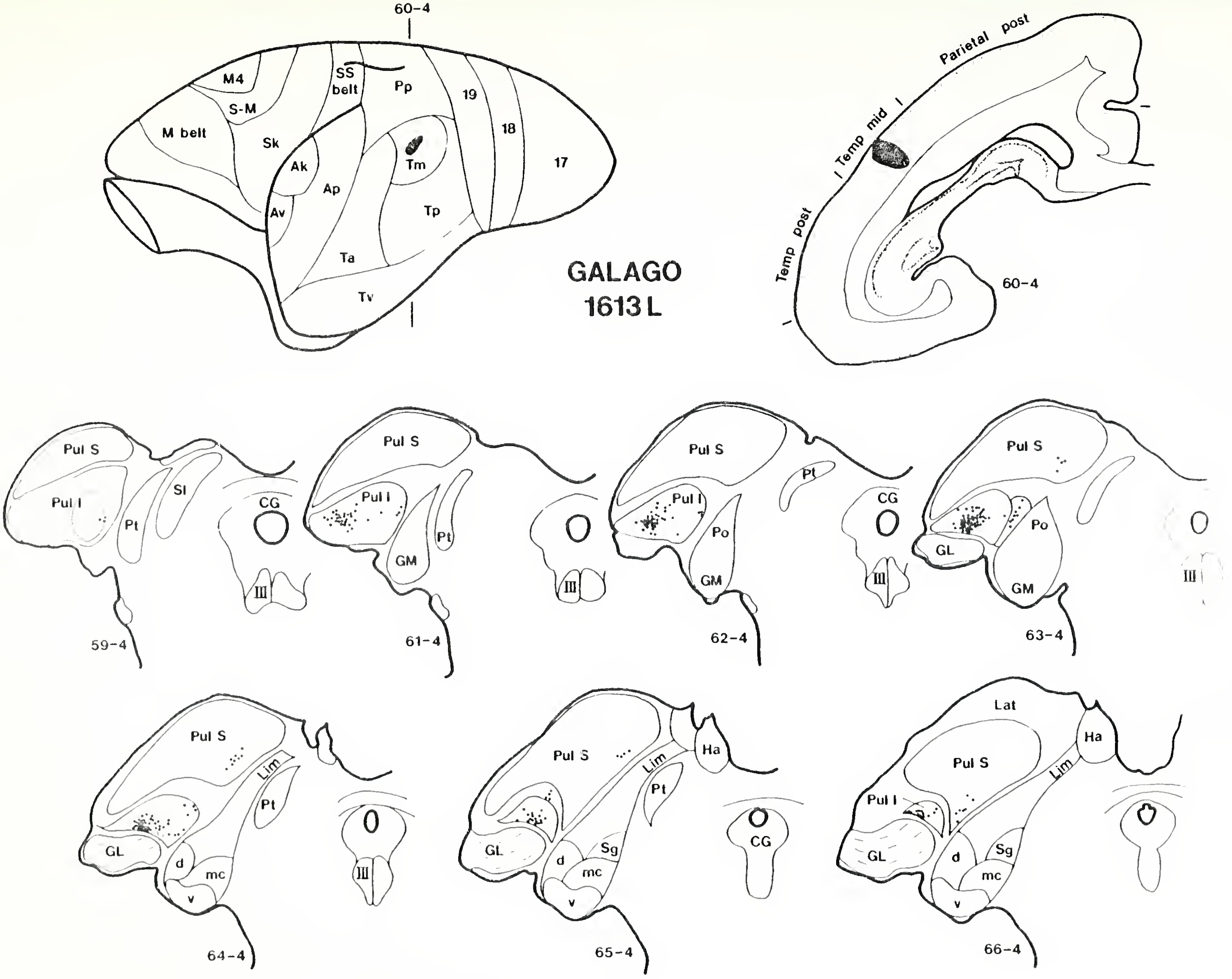
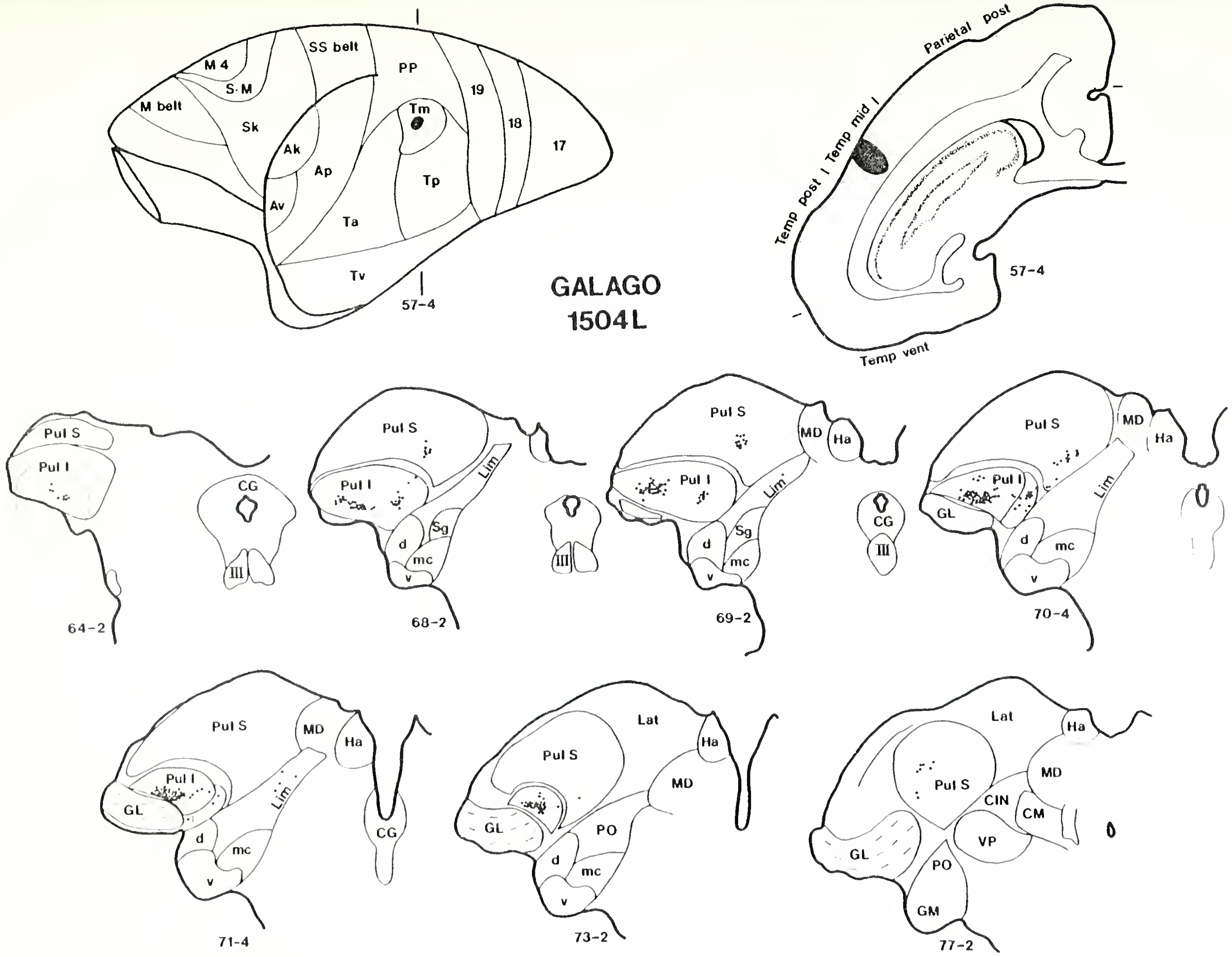

GALAGO
1613 L

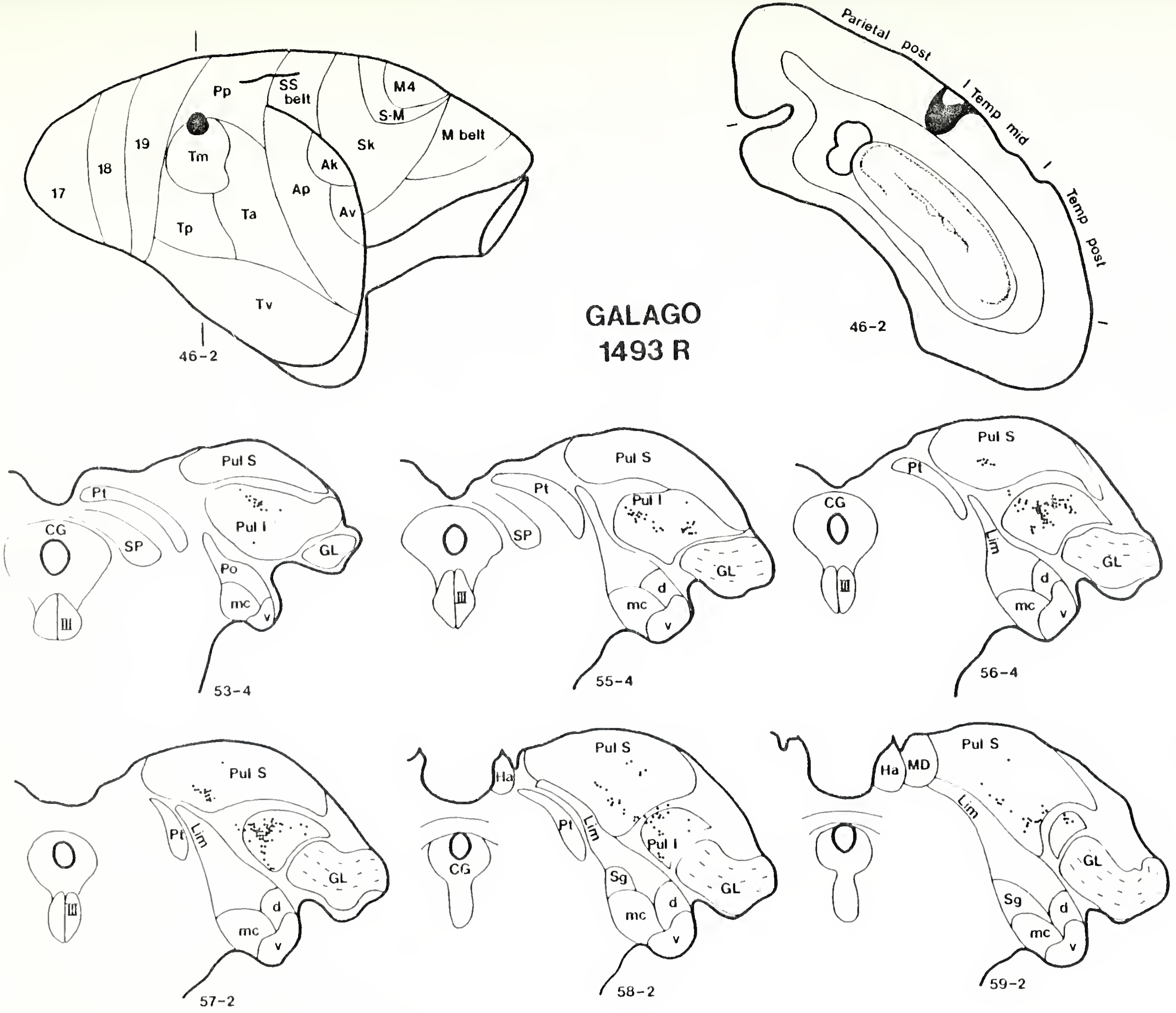
Figure 9. To show the distribution of labeled neurons in the thalamus after an injection of HRP into area Tm in Galago 1504L.



GALAGO 1504L

Figure 10. To show the distribution of labeled neurons in the thalamus after an injection of HRP into area Tm in Galago 1493R.

**GALAGO
1493 R**



dorsally located and appears to cross into the superior division where we have located the zero vertical meridian. In any case, there is certainly overlap in the distribution in this case and in the two area 18 experiments. Finally, it can be noted that in this experiment there is also some diffusion of HRP across the border in the posterior parietal area. All labeled cells remain in the pulvinar nucleus.

Injections of the anterior temporal area (Ta). Three injections of HRP were placed in area Ta, two of which are illustrated in figures 11 and 12, to underscore the reliability of the HRP method. In both experiments, 1480L and 1486L, the labeled cells formed a sheet on the ventral border of the caudal part of the inferior pulvinar nucleus (see figure 13). The locus of these labeled cells is clearly caudal and ventral to the focus of labeled cells resulting from the area Tm injections. As the sheet of labeled cells is followed rostrally it begins to rotate so the plane is no longer mediolateral but dorsoventral. Thus, in more rostral sections the labeled cells form a band not on the floor of the inferior pulvinar division but along its medial border (including the medial (Im) sector of the inferior pulvinar nucleus), and this band extends into the superior pulvinar nucleus remaining along its medial border. If the area 18 cases are taken as a way of defining the zero vertical, it would seem that the labeled cells in the two area Ta injections are located in the representation of the extreme peripheral part of the contralateral visual field.

Whether all of area Ta represents the peripheral part of the field

Figure 11. To show the distribution of labeled neurons in the thalamus after an injection of HRP into area Ta in Galago 1480L.

GALAGO
1480L

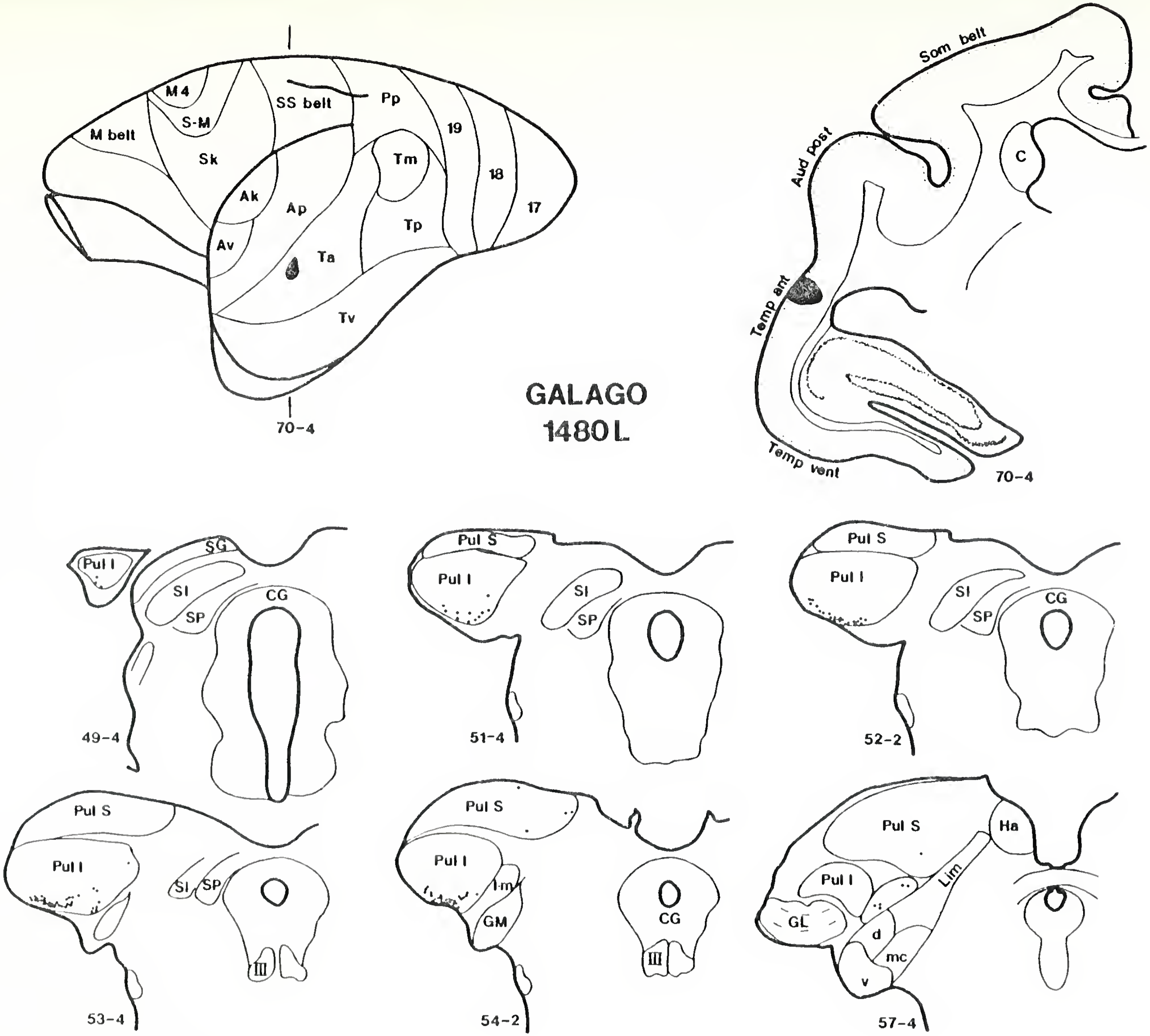


Figure 12. To show the distribution of labeled neurons in the thalamus after an injection of HRP into area Ta in Galago 1486L.

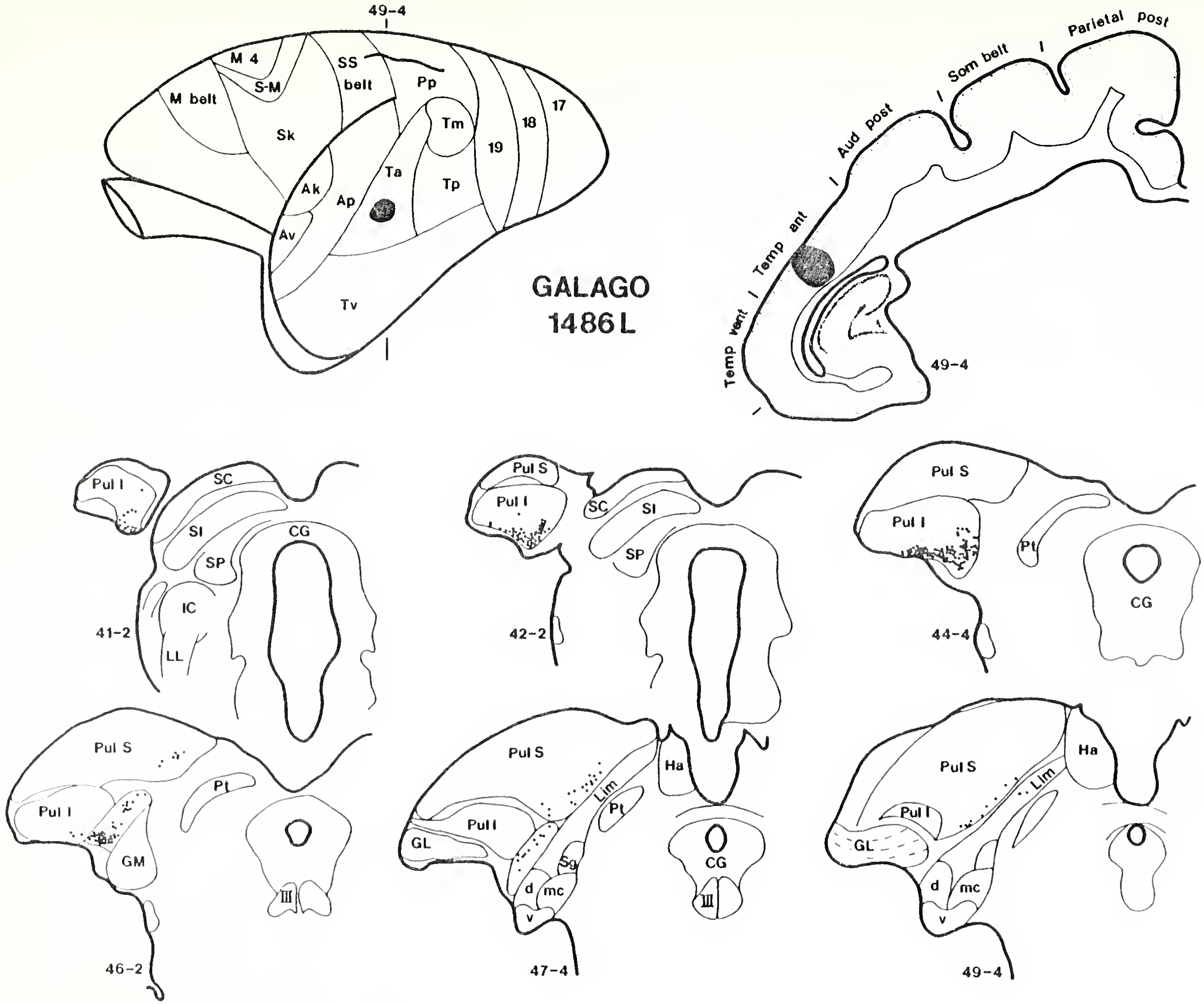
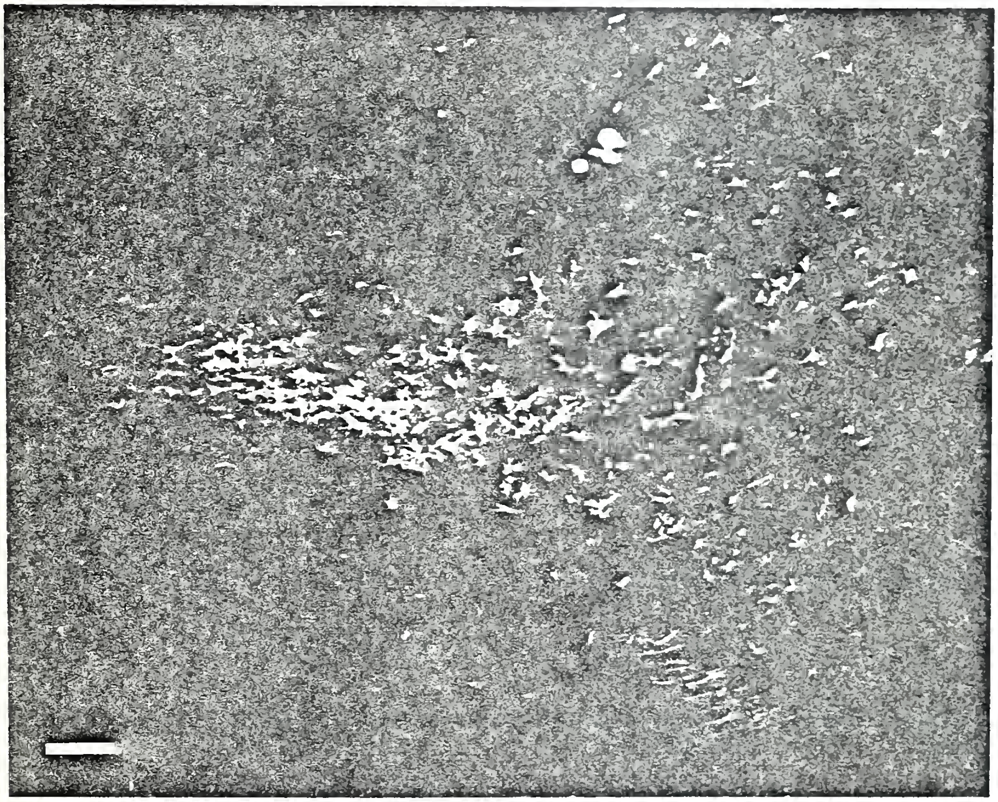

GALAGO
1486L
49-4
M 4
S-M
M belt
SS
belt
Pp
Sk
Tm
19
18
17
Ta
Tp
Ak
Ap
Av
Tv
Parietal post
Som belt
Aud post
Temp ant
Temp vent
49-4
Pul I
SC
SI
SP
CG
IC
LL
41-2
Pul S
Pul I
SC
SI
SP
42-2
Pul S
Pul I
Pt
CG
44-4
Pul S
Pul I
Pt
GM
III
46-2
Pul S
Pul I
GL
Lim
Pt
Ha
Sg
d
mc
v
CG
III
47-4
Pul S
Pul I
GL
Lim
Ha
d
mc
v
49-4

Figure 13. A dark field photomicrograph to show the pattern of labeled neurons in the inferior pulvinar after an injection of HRP into area Ta in Galago 1486L. Bar, 100 um.



and whether there is one or more than one representation of the visual field in the temporal cortex are questions we will consider below.

Injections of the ventral temporal area (Tv). The rostral portion of area Tv was injected in two experiments, and the resulting distribution of marked cells was almost identical. It is only necessary to show 1529R to illustrate this pattern (see figure 14). The greatest concentration of labeled cells was densely packed along the medial border of the caudal extremity of the superior pulvinar nucleus. The column of cells continues ventrally into the caudal part of the inferior subdivision. This sheet of cells does not reach the rostral part of the pulvinar nucleus, and only a few cells can be seen as far rostral as the middle of the superior subdivision.

Injections of the posterior temporal area (Tp). The heaviest concentration of labeled cells in the caudal extremity of the inferior pulvinar was seen after injections of area Tp. This section of the pulvinar nucleus received our special attention because it is the major target of the superficial layers of the superior colliculus, and at one point we thought it was the sole target. We also believed this sector projected to area Tm. We illustrate two cases because there are some differences between them. In the first case, Galago 1611L (illustrated in figure 15), the injection lies just below area Tm, and the caudal extent of the inferior pulvinar nucleus is dense with labeled cells throughout. Rostrally the column or sheet pattern can be recognized oriented dorsoventrally

Figure 14. To show the distribution of labeled neurons in the thalamus after an injection of HRP into area Tv in Galago 1529R.

GALAGO 1529R

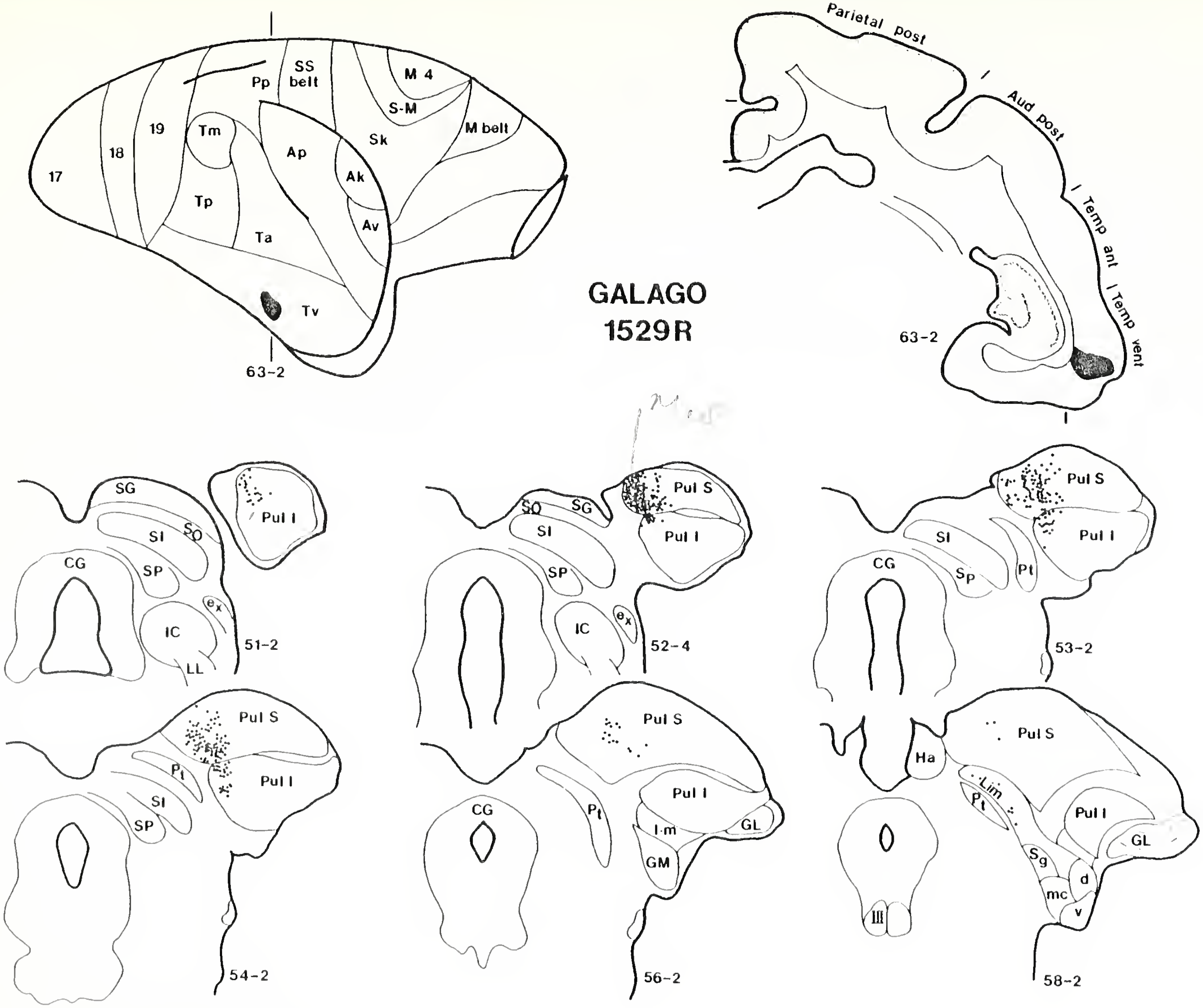


Figure 15. To show the distribution of labeled neurons in the thalamus after an injection of HRP into area Tp in *Galago* 1611L.

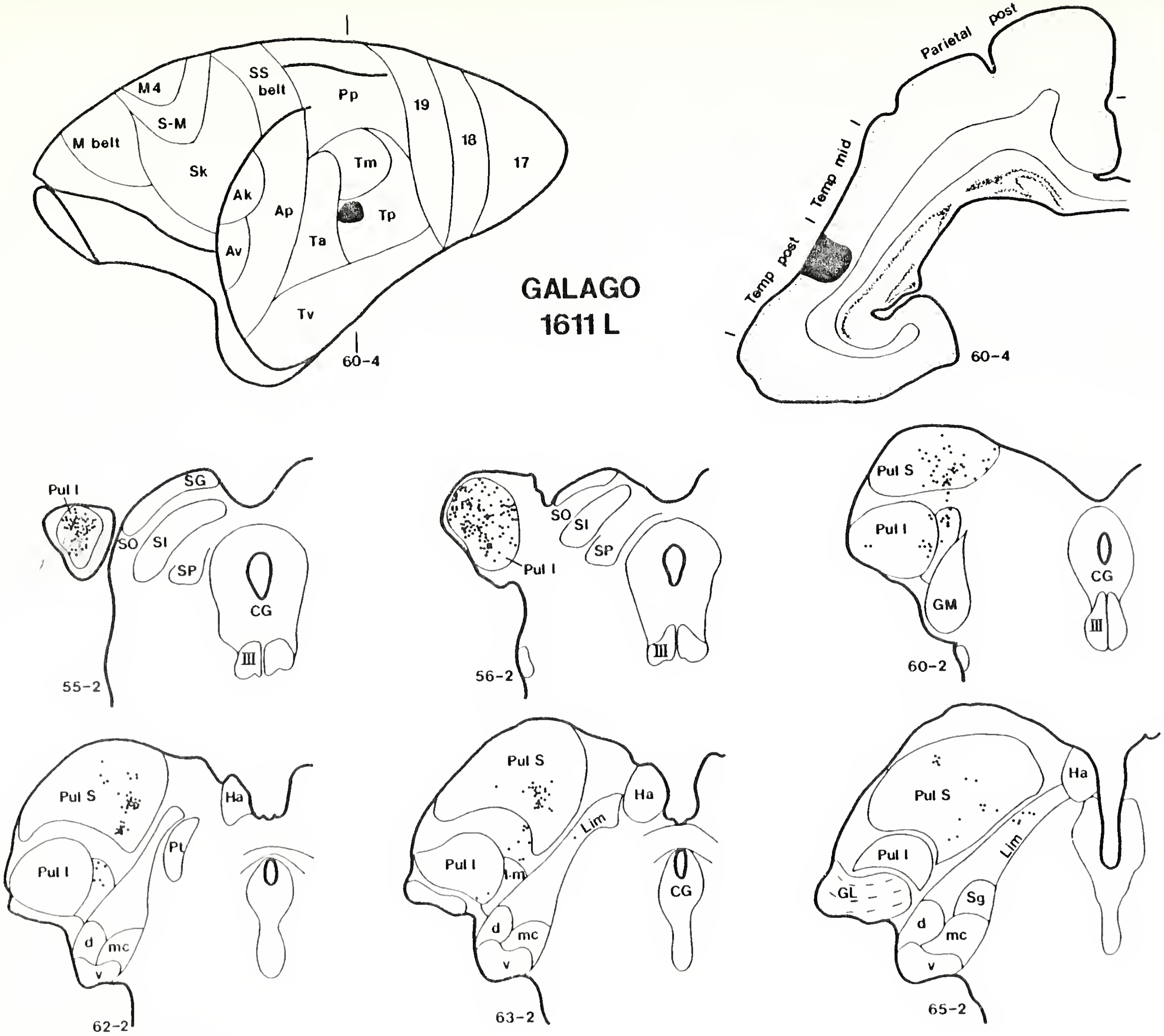
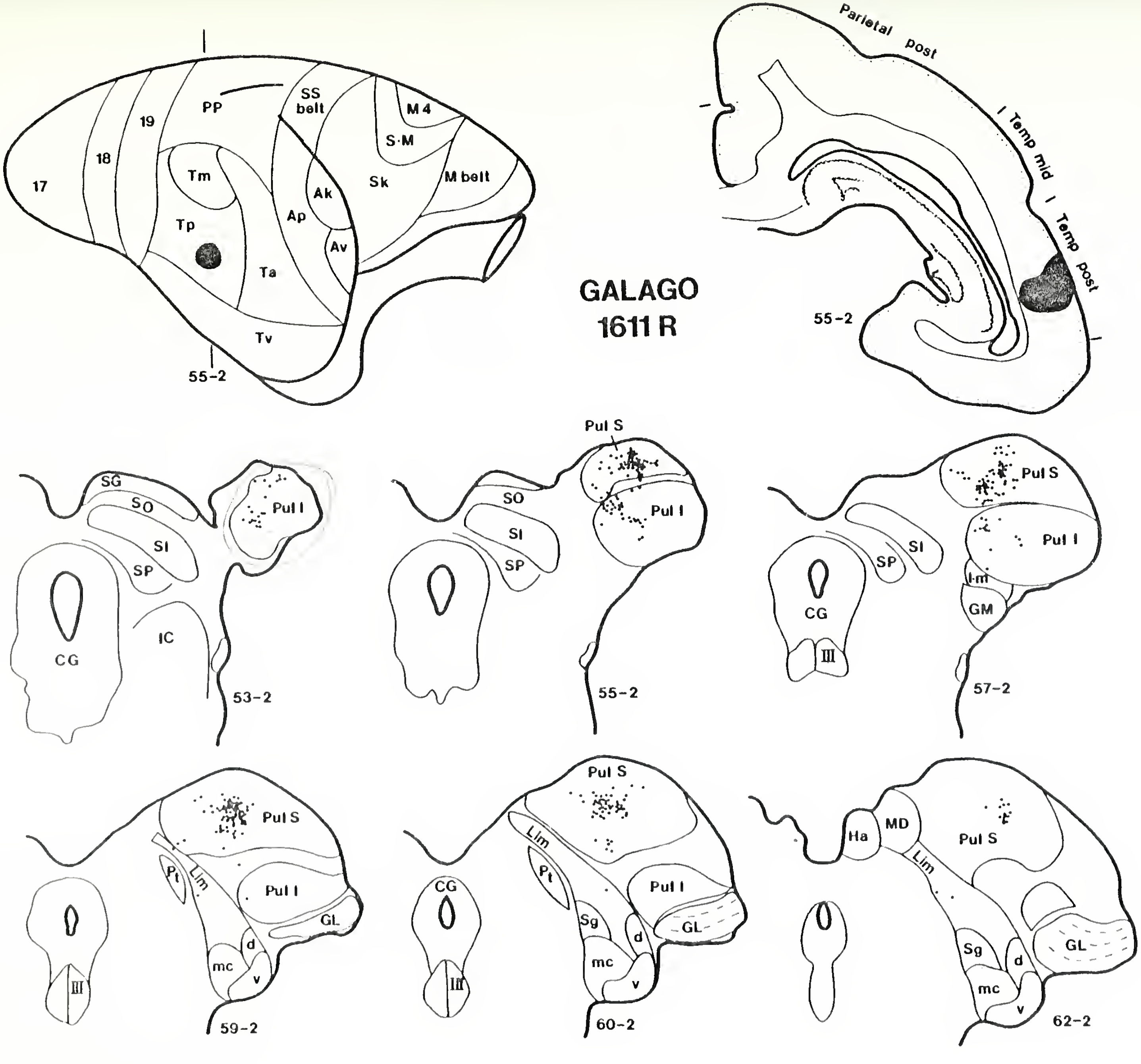

GALAGO
1611 L
M4
SS belt
Pp
19
18
17
S-M
M belt
Sk
Ak
Ap
Tm
Tp
Av
Ta
Tv
60-4
Parietal post
Temp mid
Temp post
60-4
Pul I
SG
SO
SI
SP
CG
III
55-2
SO
SI
SP
Pul I
III
56-2
Pul S
Pul I
GM
CG
III
60-2
Pul S
Ha
Pul I
Pt
d
mc
v
62-2
Pul S
Ha
Lim
Pul I
I.m
CG
d
mc
v
63-2
Pul S
Ha
Lim
Pul I
GL
Sg
d
mc
v
65-2

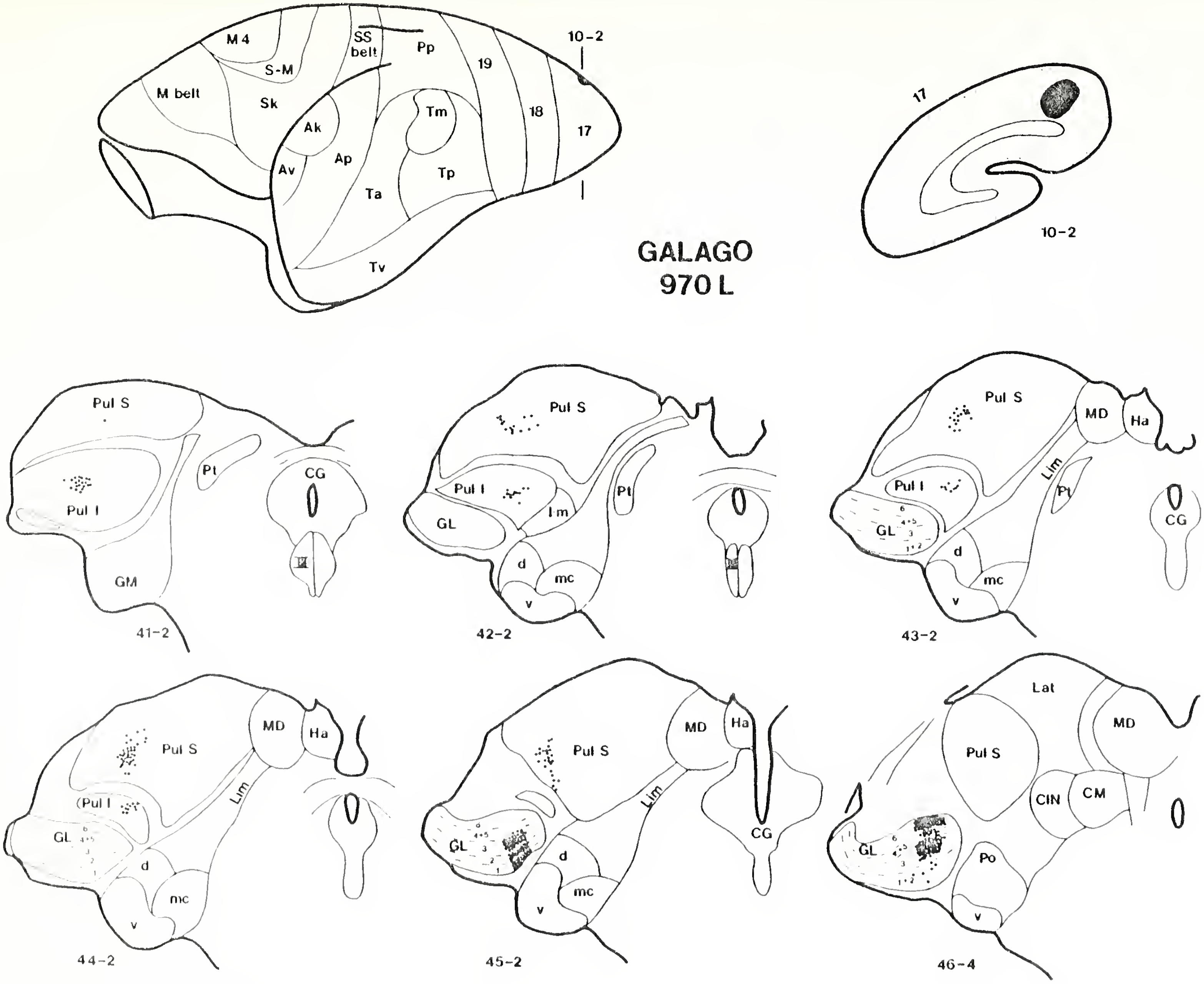
Figure 16. To show the distribution of labeled neurons in the thalamus after an injection of HRP into area Tp in Galago 1611R.


17
18
19
PP
SS belt
M 4
S·M
Sk
M belt
Tm
Tp
Ta
Tv
Ak
Ap
Av
55-2
GALAGO
1611 R
Parietal post
Temp mid
Temp post
55-2
SG
SO
SI
SP
IC
CG
Pul I
53-2
Pul S
SO
SI
SP
Pul I
55-2
Pul S
Pul I
SI
SP
I·m
GM
CG
III
57-2
Pul S
Pul I
Pt
Lim
GL
d
mc
v
III
59-2
Pul S
Lim
Pt
Pul I
CG
Sg
d
GL
mc
v
III
60-2
Ha
MD
Pul S
Lim
Sg
d
GL
mc
v
62-2

and toward the medial border of the superior pulvinar nucleus. When the injection was made more ventral in area Tp (see Galago 1611R, figure 16), the labeled cells formed two limbs of an arc much like the pattern after an 18 injection.

Injections into area 17, the striate cortex. Figure 17 shows the results of an injection into striate cortex of Galago 970L. The injection lies several millimeters behind the 17-18 border, but is quite distant from the representation of the peripheral field. This experiment makes the point that only when the HRP injection is centered in area 17 are labeled cells present in the dorsal lateral geniculate body. In this case, the labeled cells form a column extending from the dorsal border to the ventral border of the nucleus. This column of labeled cells is situated close to but not adjacent to the representation of the zero vertical meridian which lies along the dorsomedial border of the lateral geniculate body. Note that the width of the band of label markedly decreases in layers 4 and 5. Now consider the distribution of labeled cells in the pulvinar nucleus. It constitutes an arc in the rostro-caudal plane one limb of which is in each subdivision of the pulvinar complex. We assume that the two limbs meet rostrally in the superior pulvinar nucleus in section 45-2. This distribution is reminiscent of that seen after area 18 injections. Further, if the zero vertical lies along the border between the inferior and superior divisions of the pulvinar nucleus at levels 42-2 and 43-2, then the labeled cells are located close to but not on the zero

Figure 17. To show the distribution of labeled neurons in the thalamus after an injection of HRP into area 17 in Galago 970L.



GALAGO
970 L

10-2
M 4
S-M
M belt
Sk
SS
belt
Pp
19
18
17
Ak
Av
Ap
Ta
Tm
Tp
Tv
17
10-2
Pul S
Pul I
Pt
CG
GM
41-2
Pul S
Pul I
GL
Im
Pt
d
mc
v
42-2
Pul S
MD
Ha
Pul I
GL
6
4+5
3
1+2
Lim
Pt
CG
d
mc
v
43-2
MD
Ha
Pul S
(Pul I
GL
Lim
d
mc
v
44-2
MD
Ha
Pul S
GL
Lim
CG
d
mc
v
45-2
Lat
MD
Pul S
CIN
CM
GL
Po
v
46-4

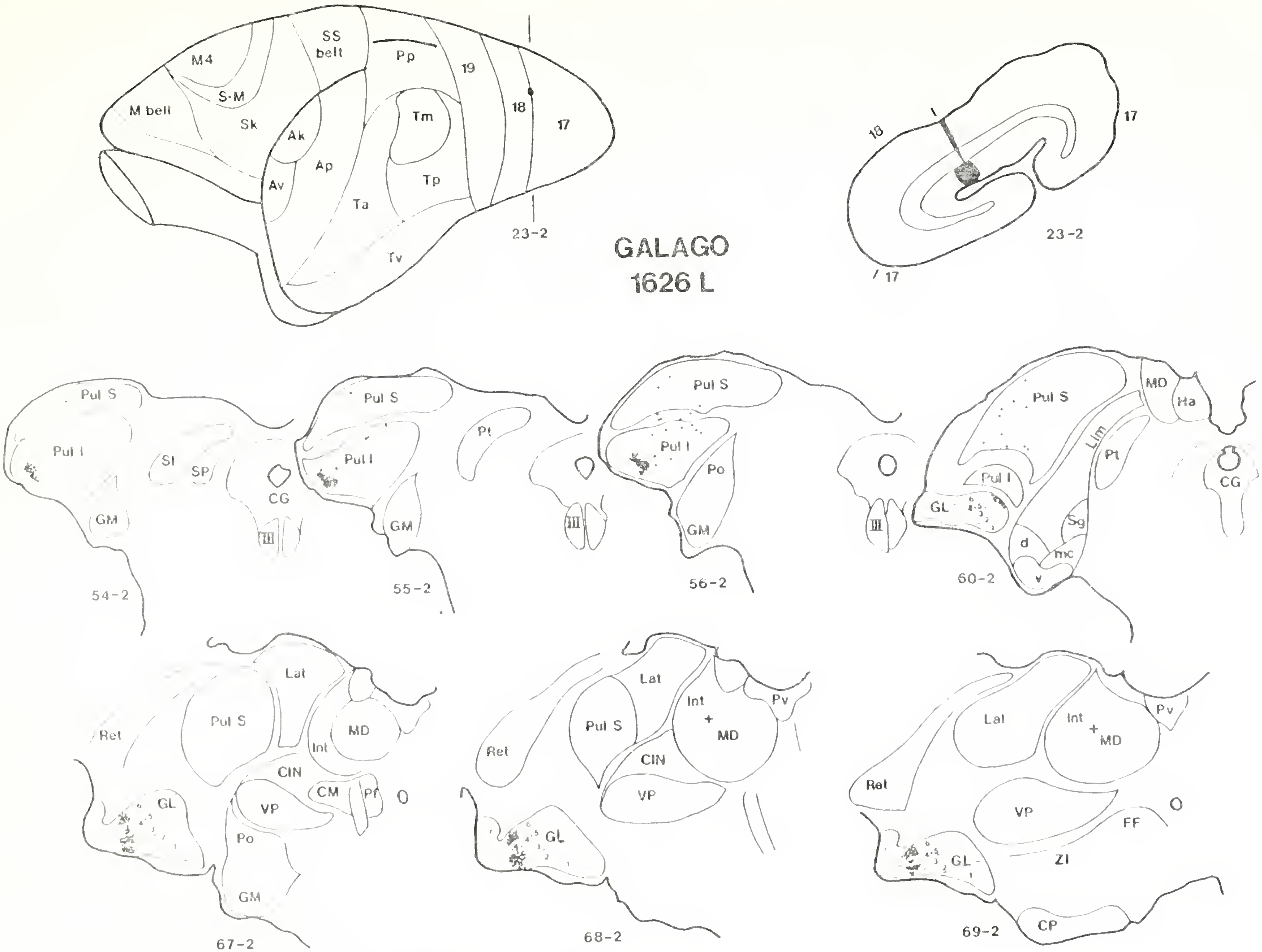
vertical meridian. If this interpretation is correct, then an injection into the representation of the periphery in 17 should stain cells at the ventral border of the inferior pulvinar nucleus, in the position where labeled cells are located after area Ta injections.

In experiment 1626L, illustrated in figure 18, we attempted to inject the cortex of the calcarine fissure by penetrating the lateral wall. A photomicrograph of this injection is shown in figure 19. The point of penetration turned out to be precisely on the 17-18 border. A very small amount of HRP escaped along the track, and, as a result, few cells were labeled in the dorsal lateral geniculate body precisely on the zero vertical meridian (see section 60-2). Also, a few stained cells were scattered near the border between the two major divisions of the pulvinar nucleus. This is just the locus of labeled cells after the injection of area 18.

A second column of labeled cells was found laterally in the dorsal lateral geniculate body, shown in sections 67-2 and 68-2, which is close to the monocular segment and in a region of the dorsal lateral geniculate body representation of the peripheral field. Again, the column of labeled cells diminished in layers 4 and 5 and this point is illustrated in figure 20. The main point of this experiment is the locus of labeled cells at the ventral base of the inferior pulvinar nucleus (see sections 54-2, 55-2, and 56-2).

We conclude from these experiments that both area 17 and the

Figure 18. To show the distribution of labeled neurons in the thalamus after an injection of HRP into area 17 in Galago 1626L.



GALAGO 1626 L

Figure 19. A photomicrograph to show an injection of HRP into that portion of area 17 lying in the depth of the calcarine fissure in Galago 1526L. Bar, 1 mm.

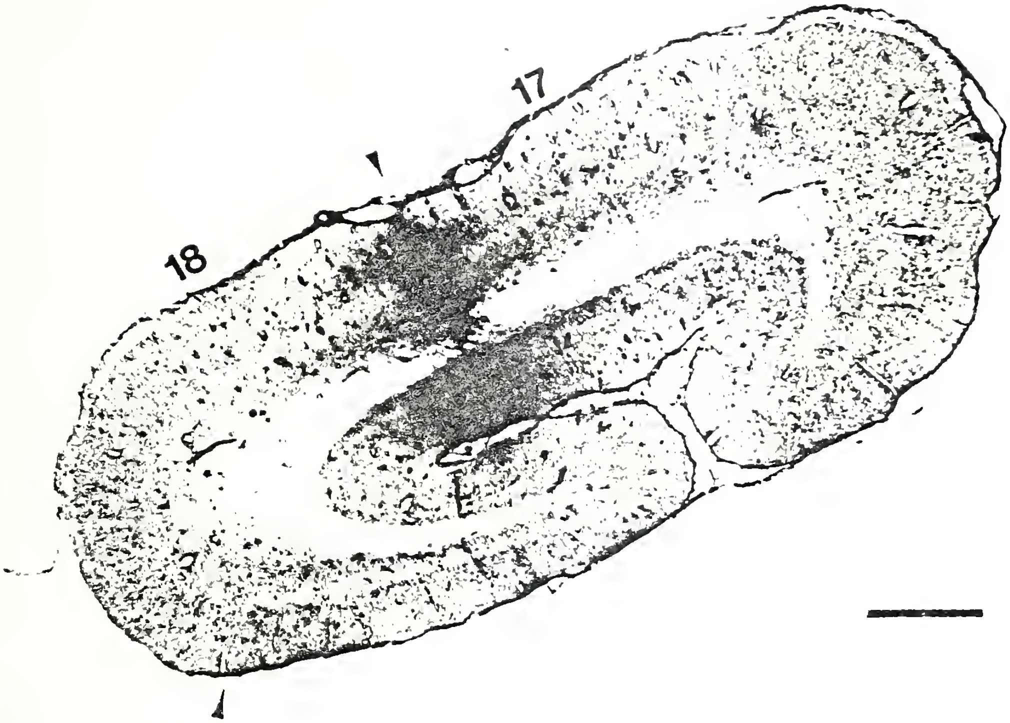
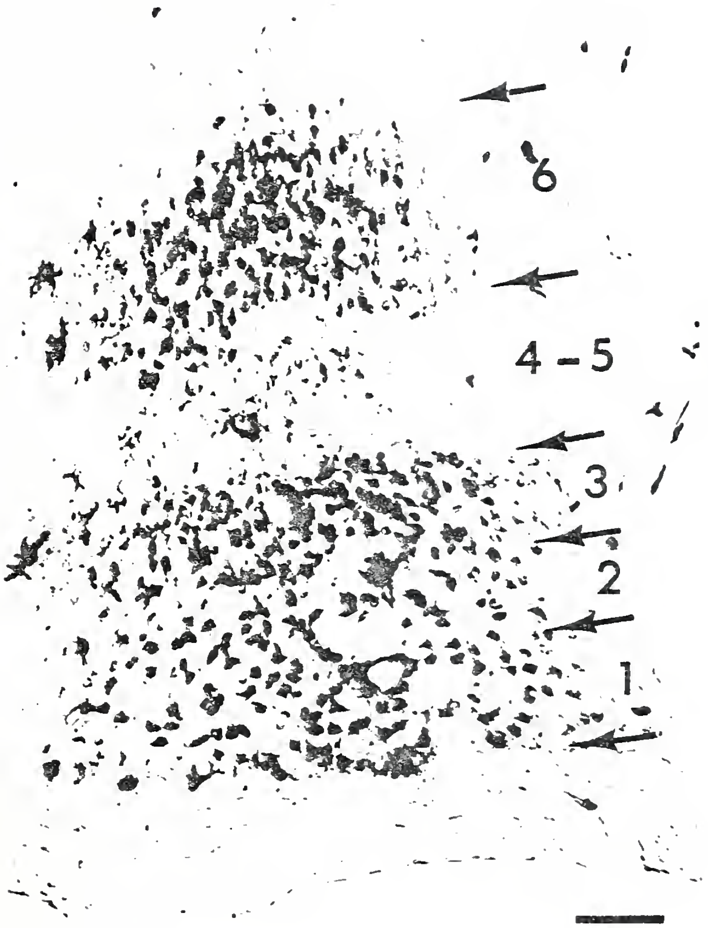

18
17

Figure 20. A photomicrograph to show the column of labeled cells in the dorsal lateral geniculate body after an injection of HRP into area 17 in *Galago* 1526L. Note that the column of labeled cells diminishes in layers 4 and 5. Bar, 100 um.


6
4 – 5
3
2
1

cortex intercalated between area 17 and the auditory cortex receive a separate projection from the entire pulvinar complex. In addition, these results contribute to our knowledge of the representation of the visual field on the pulvinar nucleus. Thus, the representation of the contralateral visual field in the inferior pulvinar is such that the zero vertical meridian lies along the common border formed by the two major subdivisions of the pulvinar nucleus. This suggests that the visual periphery is represented along the ventral border of the subdivision. Finally, we believe that the representation of the visual field in the superior pulvinar may well be a mirror image of the organization just described for the inferior pulvinar.

II. Projections from the Cortex and Brainstem to the Pulvinar Nucleus Studied with the Horseradish Peroxidase Method

Introduction

Following lesions restricted to the superficial layers of the superior colliculus of *Galago*, Glendenning et al. ('75) observed degenerating fibers entering and terminating only in the caudal portion of the inferior pulvinar nucleus. The rostral half of the inferior pulvinar, as well as the entire superior pulvinar, were almost completely free of degeneration. In an effort to determine whether these subdivisions of the pulvinar nucleus were the recipients of fibers from other ascending sensory paths, small lesions were placed in the pretectal nuclei (Raczkowski,

unpublished). The results indicated that the pulvinar is not a target of the pretectum. From these experiments it was concluded that truly intrinsic subdivisions of the pulvinar may have evolved with the origin of primates (Glendenning et al., '75).

However, we now know that the anterograde degeneration method, by itself, is not as sensitive an indicator of connections as is the method of retrograde transport of HRP. Thus, to advance the inquiry, injections of HRP were placed into the pulvinar of *Galago senegalensis*.

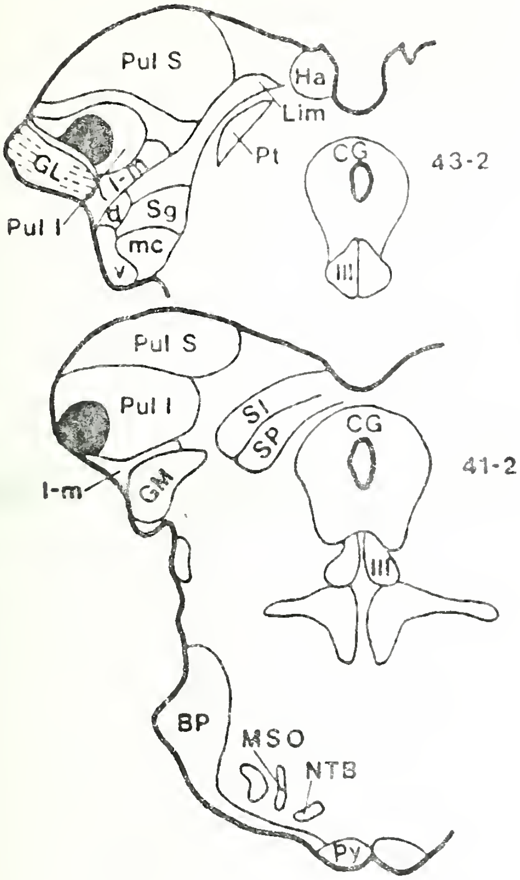
The results of these experiments will show that the entire pulvinar nucleus is the recipient of fibers from the superficial layers of the superior colliculus. At the same time, these injections reveal the distribution and laminar origin of descending projections from the cortex to the pulvinar nucleus.

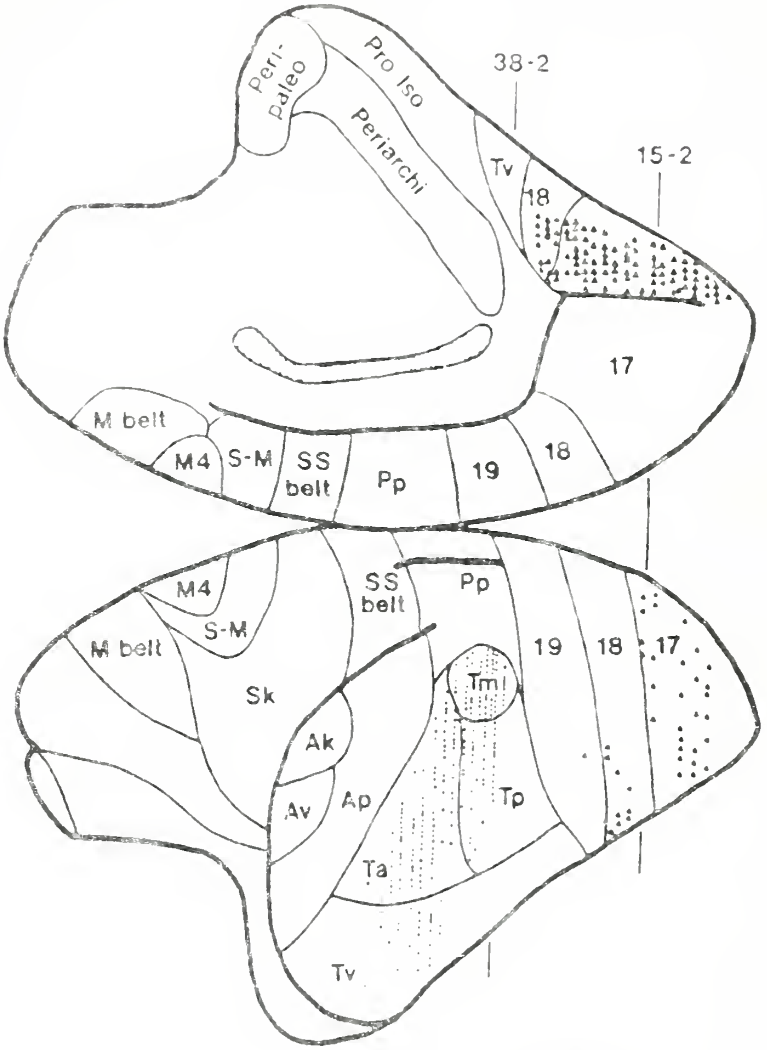
Experimental Results

Part 1: Effects of Injecting HRP into the Inferior Pulvinar Nucleus

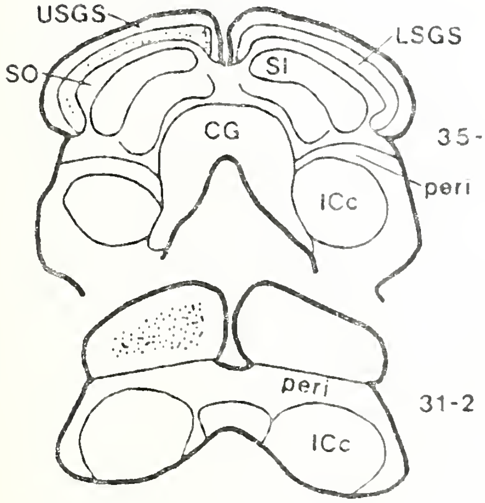
Figure 21 (*Galago* 1141R) shows the result of an injection of HRP into that portion of the inferior pulvinar nucleus which earlier had been shown to be the recipient of tectal fibers. The injection is this case, depicted in black in the upper left portion of figure 21, is situated ventrolaterally in the subdivision and extends nearly the entire length of the nucleus. Although this injection is rather large, at no point did the brown stain diffuse beyond the borders of the inferior pulvinar nucleus. One

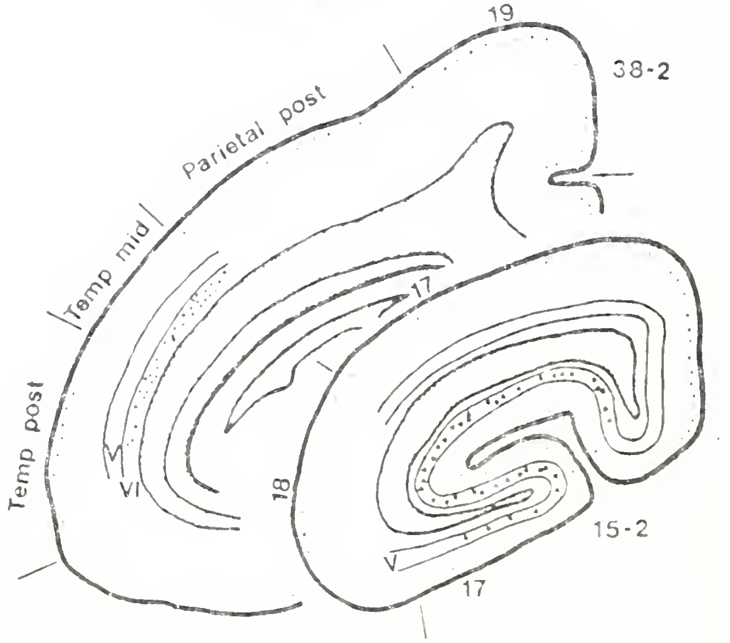
Figure 21. To show the distribution of labeled neurons in the brain stem and cortex after an injection of HRP into the pulvinar nucleus in Galago 1141R. The following convention applies to the next 9 line drawings. The locus of the injection is depicted in black in the upper left portion of the figure. Labeled neurons in the brain stem are depicted by solid dots in the lower left portion of the figure. The distribution of labeled neurons in the cortex is shown in the upper right portion of the figure. Labeled cells in layer VI are depicted by solid dots while labeled cells in layer V are depicted by filled triangles. Representative frontal sections to show the locations of labeled neurons are illustrated in the lower right portion of the figure.





GALAGO 1141 R



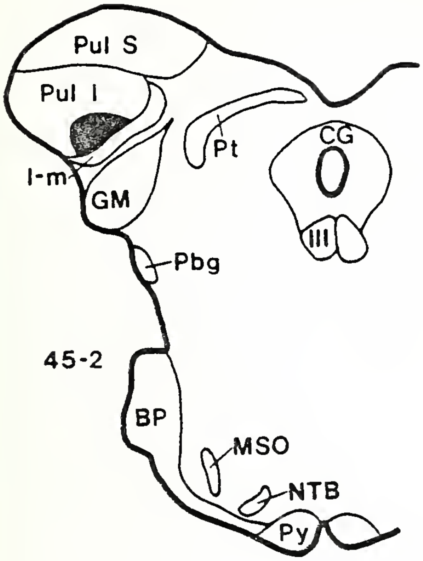


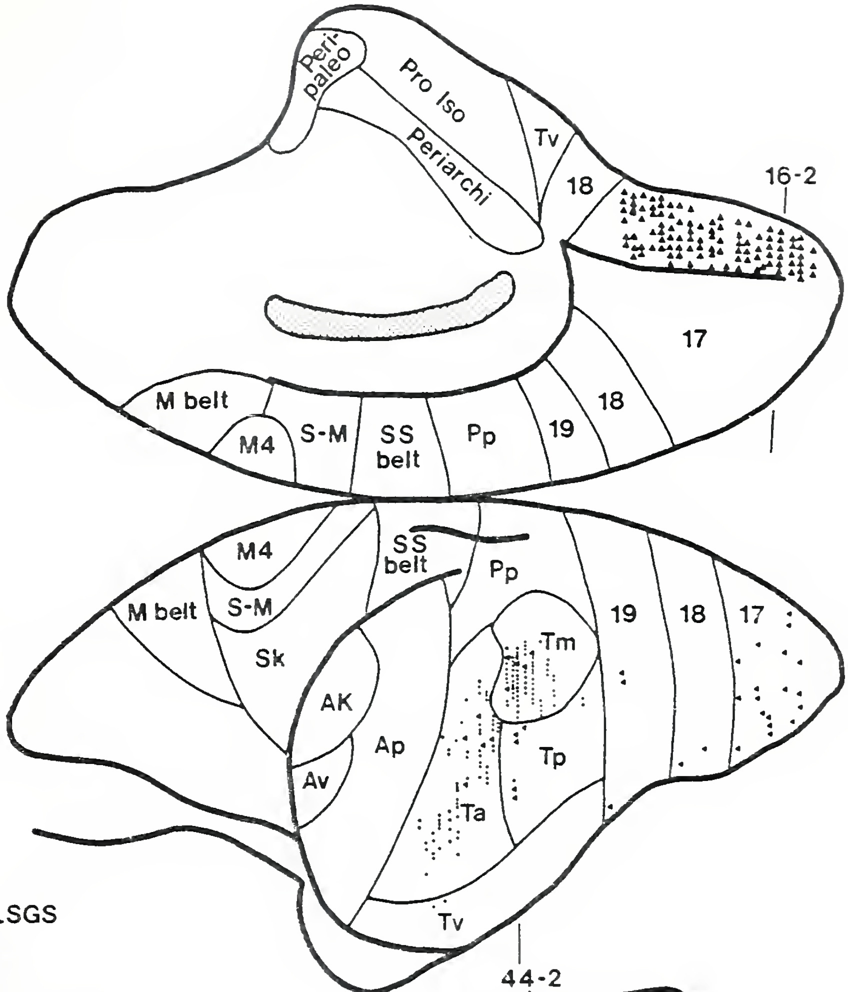
chief result of injecting HRP into the inferior pulvinar nucleus is illustrated in the lower left portion of figure 21. In the superior colliculus, labeled cells were observed only in the lower half of stratum griseum superficiale while the upper half of stratum griseum superficiale was free of labeled cells. The heaviest concentration of HRP filled neurons is in the caudal portion of the superior colliculus. As the labeled cells are followed rostrally through successive levels, the labeled cells shift medially.

The HRP method is useful not only in identifying the cells of origin of brain stem inputs to the inferior pulvinar nucleus, but also in providing the opportunity to examine the laminar origin and distribution of cortical descending pathways to the inferior pulvinar nucleus. These results are summarized in the right half of figure 21, and two findings should be emphasized. First, labeled cells are observed in layer VI of the temporal lobe, and these cells are represented by dots. In this experiment, the distribution of labeled cells is heaviest in areas Tm and Ta; in addition, areas Tp and Tv also contain labeled cells. A second main finding is that another cluster of labeled cells is observed in layer V of area 17 and this label is depicted by filled triangles. In this experiment, the labeled cells in area 17 are concentrated along the ventral bank of the calcarine fissure. No labeled cells were located outside the visual field, as defined in the previous section.

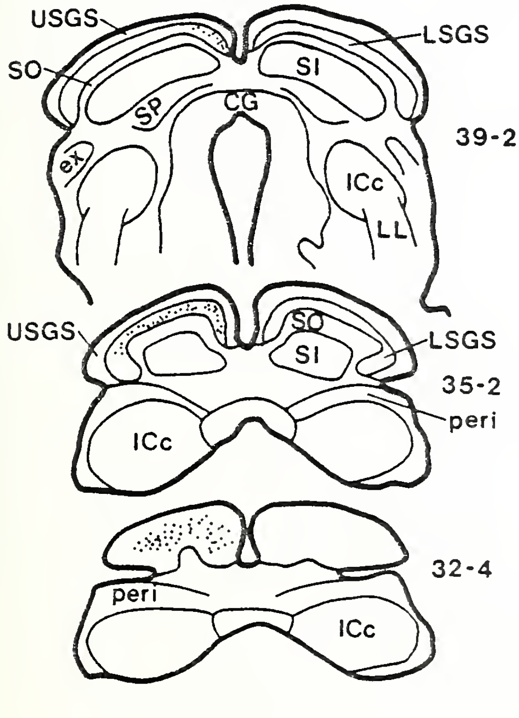
The next experiment, *Galago* 1199R (see figure 22), illustrates

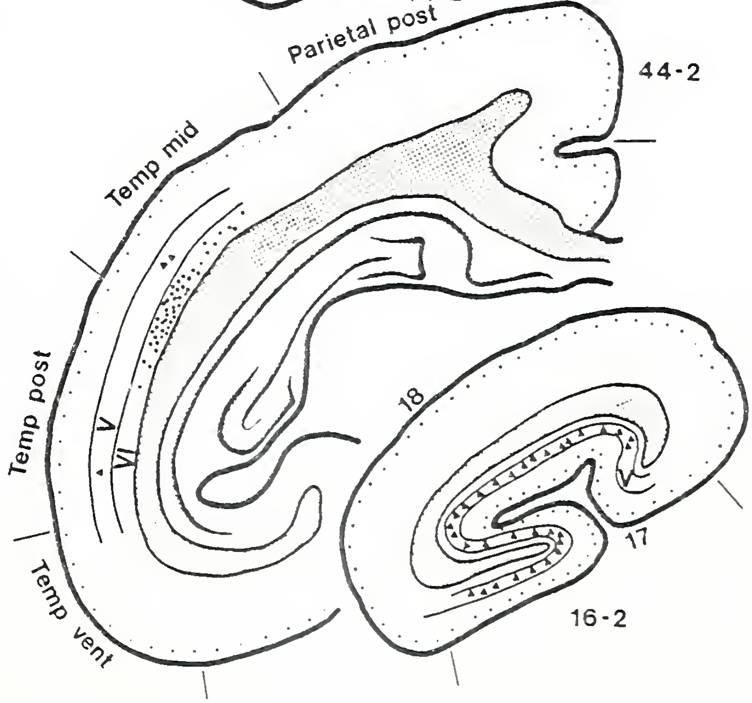
Figure 22. To show the distribution of labeled neurons in the brain stem and cortex after an injection of HRP into the inferior pulvinar nucleus in *Galago* 1199R.





GALAGO 1199 R





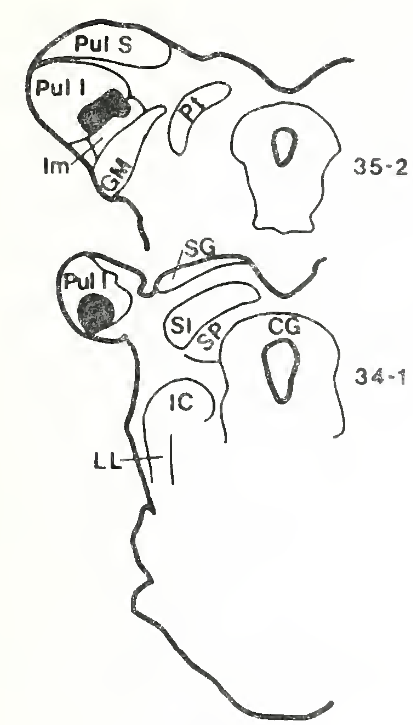
another HRP injection centered in the caudal and ventral portions of the inferior pulvinar nucleus. The distribution of labeled cells in the superior colliculus and neocortex of this animal is identical to that described in the previous experiment and serves as a check of the reliability of the HRP method.

Briefly, in the superior colliculus, HRP filled neurons were concentrated in the caudal portion of the nucleus and were distributed along the entire mediolateral dimension of the lower half of stratum griseum superficiale. Advancing rostrally, the distribution of labeled cells again shifted medially.

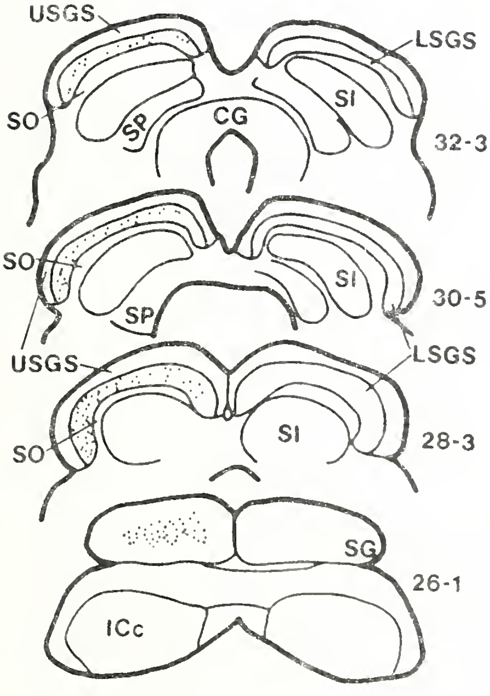
In the cortex, two discontinuous clusters of labeled cells were observed. The labeled cells in layer VI were located principally in areas Tm and Ta, with a few scattered cells present in area Tp. Finally, labeled layer V pyramid cells in area 17 were distributed along the lower bank of the calcarine fissure.

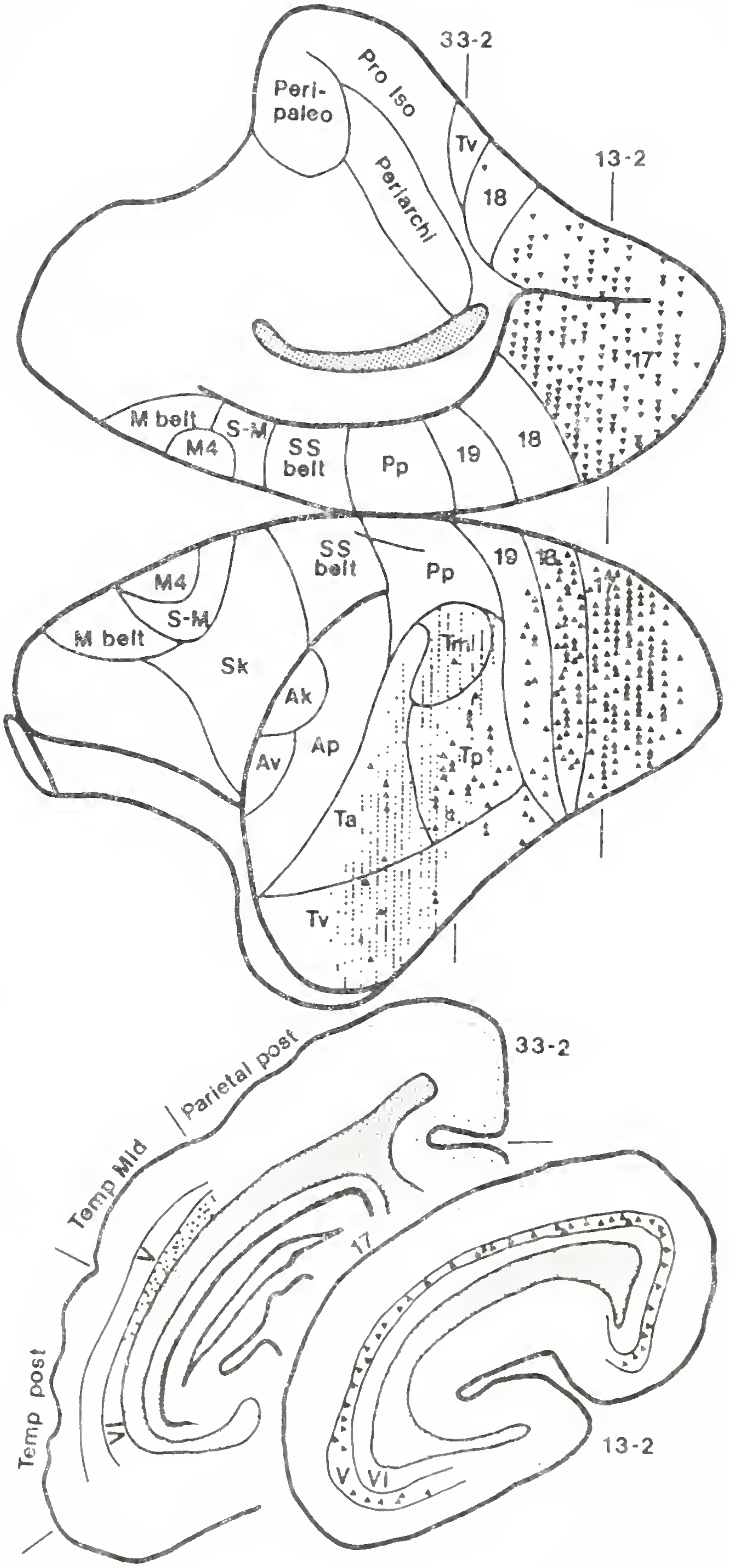
In *Galago* 1143R (see figure 23), a large amount of HRP was injected into the ventral and *medial* portion of the caudal inferior pulvinar nucleus. This experiment makes the point that the visual projections from the tectum and striate cortex are organized along a mediolateral dimension in the inferior pulvinar nucleus. In the colliculus, for example, labeled cells were once again located in the caudal one-third of the nucleus. However, in contrast to the previous two experiments, the labeled cells are distributed along the *lateral* portion of the lower half of

Figure 23. To show the distribution of labeled neurons in the brain stem and cortex after an injection of HRP into the inferior pulvinar nucleus in Galago 1143R.



GALAGO 1143 R





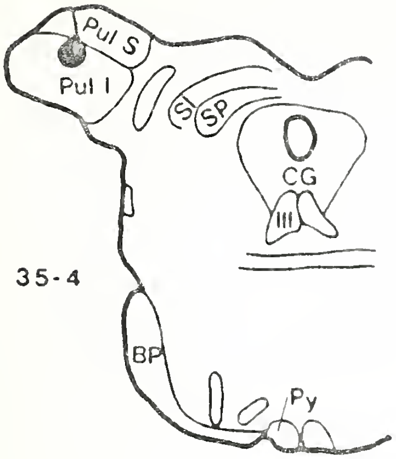
stratum griseum superficiale.

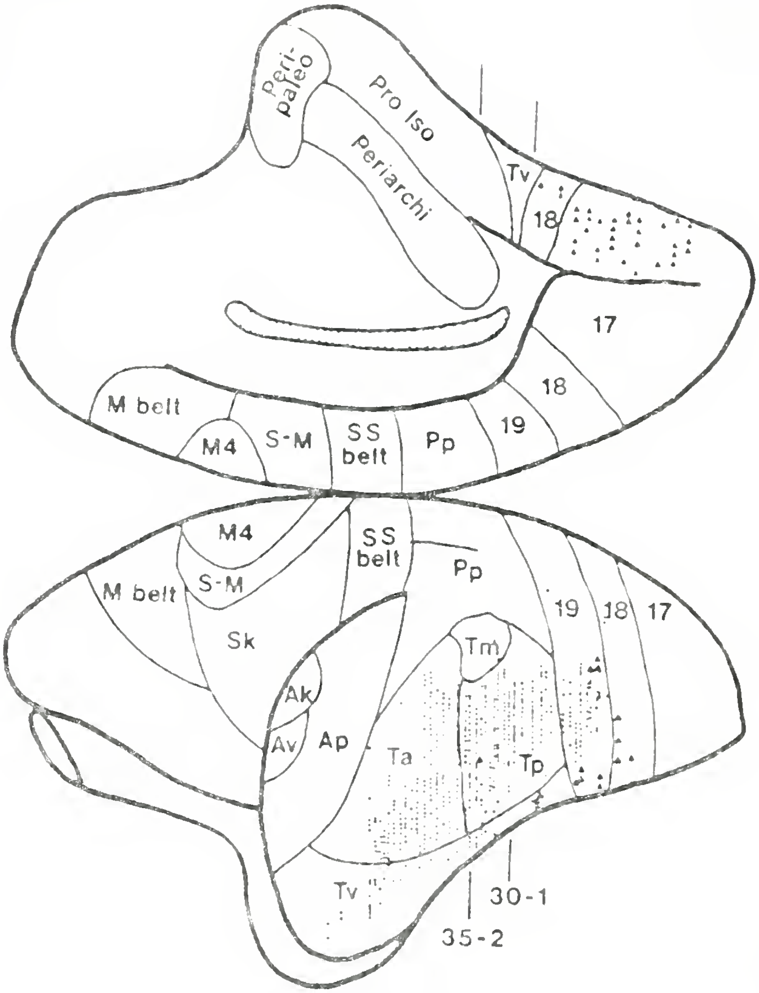
In the cortex, a sheet of labeled cells in layer VI was observed extending in a continuous manner from area Tm to area Tv. Reflecting the medial shift in the position of the injection in the experiment, the focus of the layer V label in area 17 has now shifted onto the dorsal and lateral surface of the cortex, in the representation of the upper visual field. Some layer V pyramid cells were labeled in areas 18 and 19 and Tp; however, the concentration does not in any way approach that observed in the striate cortex.

The next two experiments summarize the effect of injecting HRP into the dorsal portions of the inferior pulvinar nucleus. In the first of these experiments, Galago 1270R (see figure 24), the injection is situated dorsal and lateral in the nucleus. In the superior colliculus, labeled cells are observed in the medial portion of the lower half of stratum griseum superficiale, confirming the relationship established in experiments 1141R and 1199R. However, the concentration of labeled cells is located rostrally in the tectum in the representation of central vision. This experiment makes the point that, as the injection site shifts dorsally in the inferior pulvinar, the labeled cells in the colliculus are located nearer the representation of the zero vertical meridian.

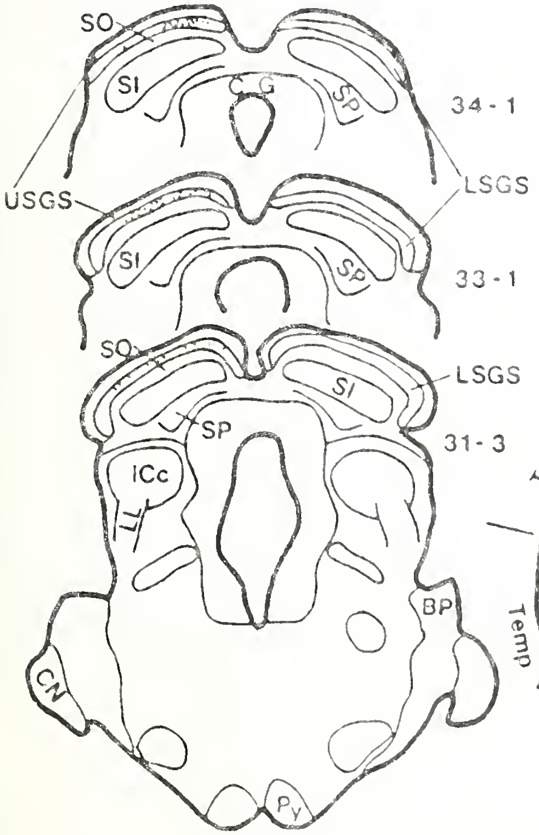
Turning to the cortex, the sheet of labeled cells in layer VI has also moved within the temporal field. In contrast to the previous three experiments, the heaviest concentration of labeled cells is located within

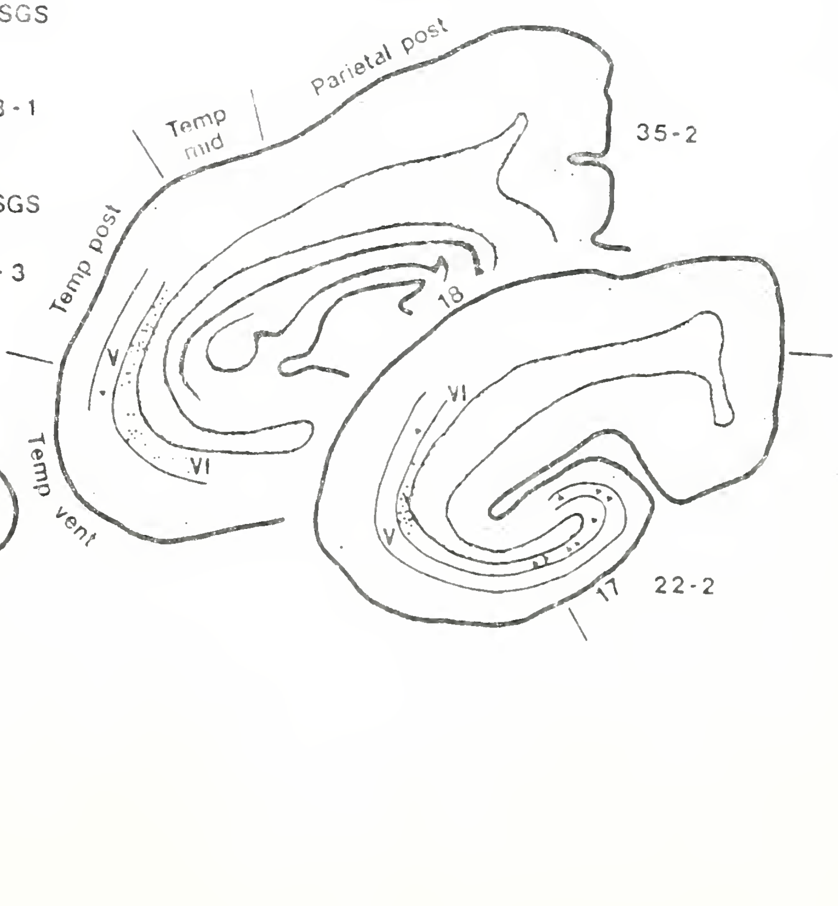
Figure 24. To show the distribution of labeled neurons in the brain stem and cortex after an injection of HRP into the inferior pulvinar nucleus in Galago 1270R.





GALAGO 1270 R





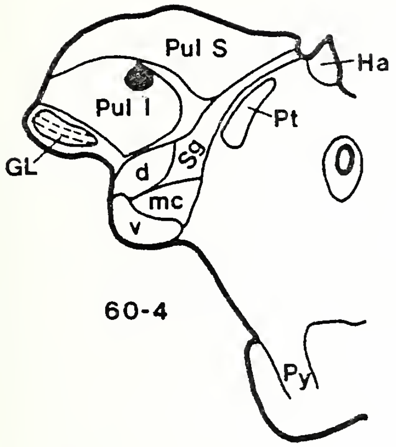
area Tp. Additional HRP filled neurons are located in areas Ta, Tv, and area 19. It is important to note that the labeled cells abut the border of area Tm where the representation of the zero vertical meridian is located. A second cluster of labeled cells is again observed in the striate cortex. Confirming the pattern established in the previous experiments, all of the labeled cells are confined to layer V.

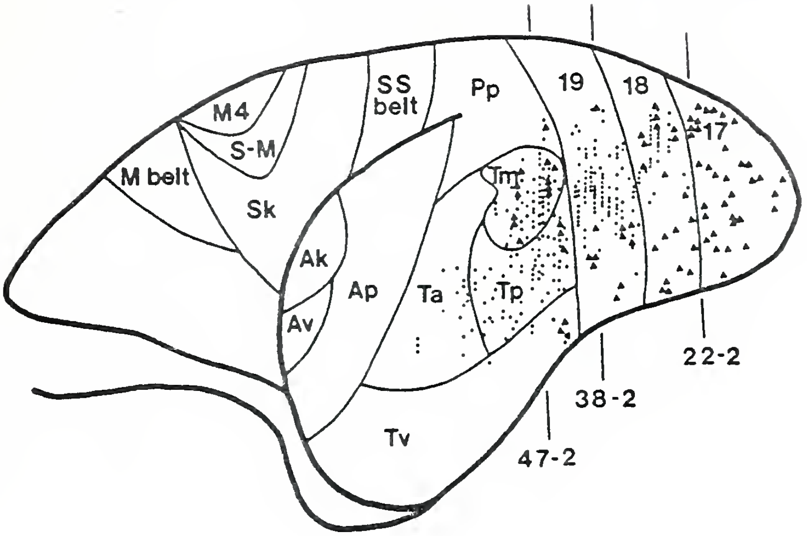
In Galago 1318R, illustrated in figure 25, the injection area has shifted mediorostrally with respect to the previous injection (Galago 1270R). Corresponding to this shift, the labeled cells in the superior colliculus are now located in the rostrolateral portion of the lower half of stratum griseum superficiale.

Regarding the distribution of labeled cells in the cortex, the rostral movement of the injection is duplicated in a shift of the sheet of labeled layer VI neurons. In this experiment, the focus of labeled VI cells is located primarily in area 19. Additional HRP filled neurons are located in area Tp and area 18. As in the previous experiment, the distribution of labeled cells stops abruptly at the border of area Tm. The medial position of the injection site in this experiment is reflected in the presence of labeled layer V neurons on the lateral surface of area 17.

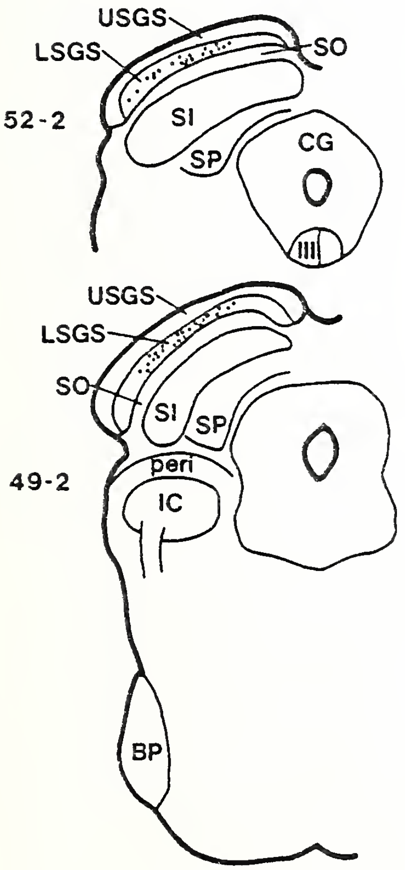
The final experiment in this section, Galago 1315L (see figure 26), illustrates the effect of injecting a small amount of HRP into the rostral pole of the inferior pulvinar nucleus. This experiment makes one very important point: The entire inferior pulvinar nucleus is the recipient of

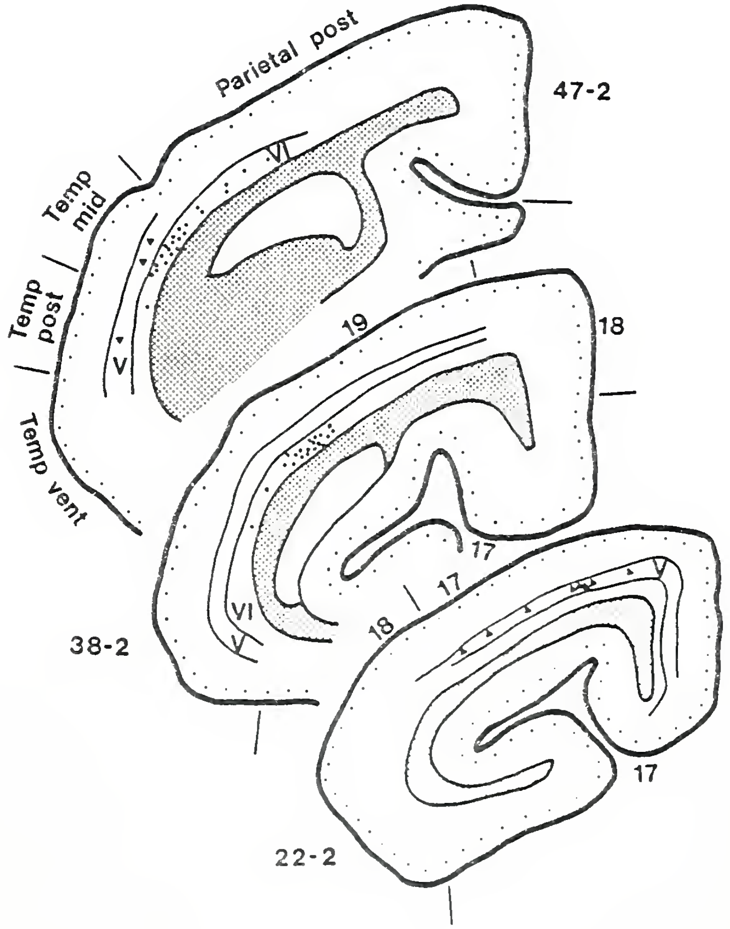
Figure 25. To show the distribution of labeled neurons in the brain stem and cortex after an injection of HRP into the inferior pulvinar nucleus in *Galago* 1318R.





GALAGO 1318 R



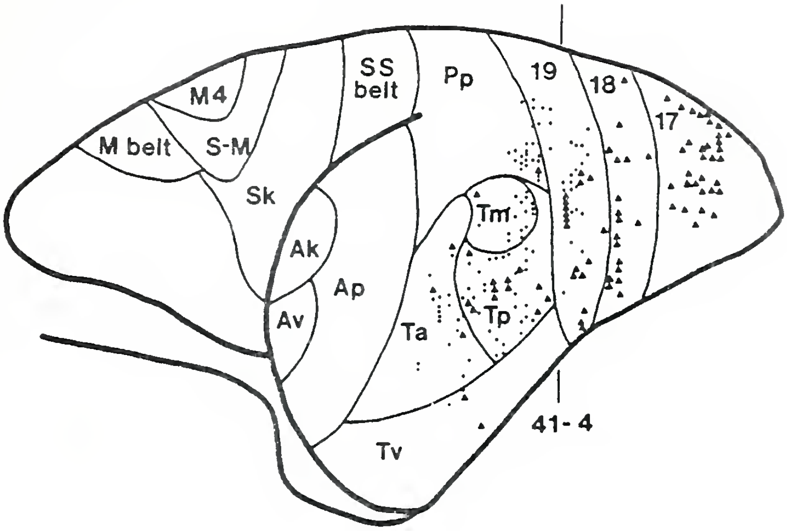


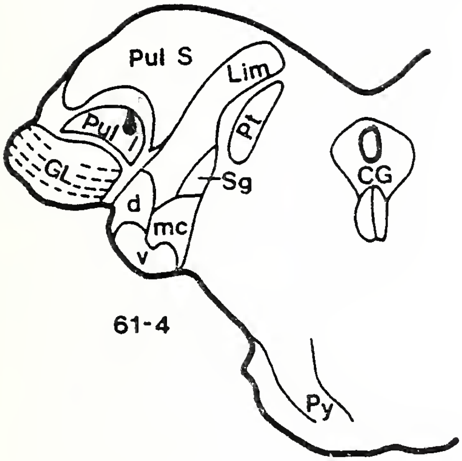
ascending sensory input from the tectum. In the previous five cases presented, the HRP injection always involved some portion of the tecto-recipient zone, as defined by anterograde degeneration methods. Thus, it came as no surprise that labeled cells were observed in the superior colliculus. In contrast to the previous experiments, the injection in this experiment (see upper left portion of figure 26) is located in a portion of the inferior pulvinar that we had not found terminal degeneration after lesions of the superior colliculus, and yet, labeled cells are identified in the lower half of stratum griseum superficiale of the superior colliculus. This point is illustrated in the lower left portion of figure 26. Note that the position of the labeled cells follows the organization described in the previous experiments. The number of labeled cells in the colliculus is fewer than in the other experiments presented, no doubt reflecting the small size of the injection as well as the intensity of the projection from the tectum.

In the cortex, labeled layer VI neurons were concentrated primarily in area 19. Additional HRP filled neurons are located in areas Ta, Tp, Tv, Tm, and Pp. Scattered among this sheet of labeled layer VI neurons are a few labeled layer V pyramids. This point is emphasized in the frontal section in the lower right portion of the figure. However, as in all previous experiments, the heaviest concentration of labeled layer V pyramid neurons is located in area 17.

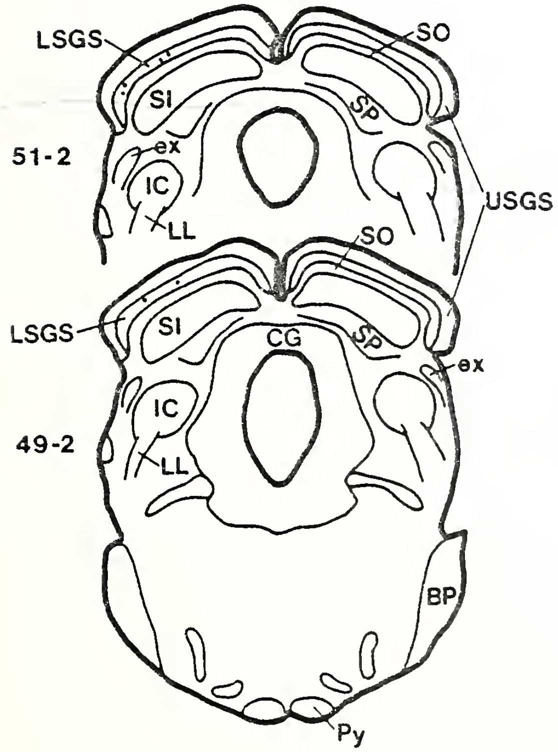
Summarizing these six experiments, several main points need to

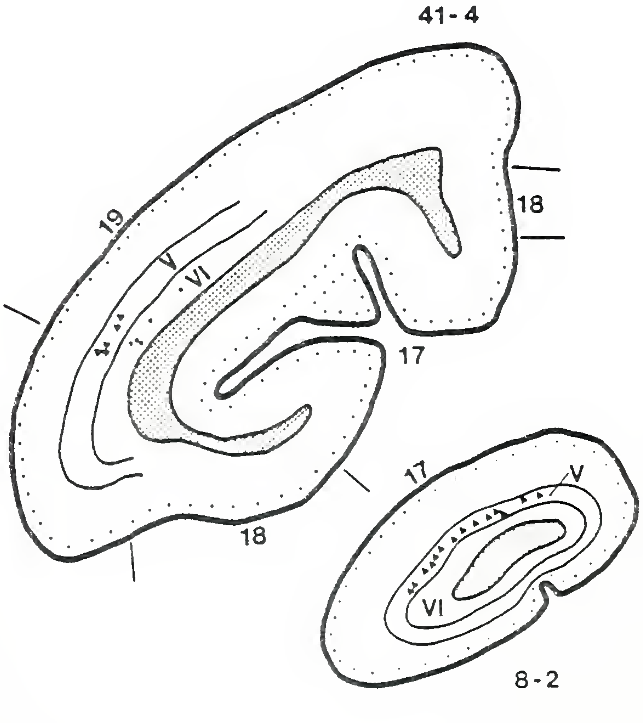
Figure 26. To show the distribution of labeled neurons in the brain stem and cortex after an injection of HRP into the inferior pulvinar nucleus in Galago 1315L.





GALAGO 1315 L





be emphasized. First, all portions of the inferior pulvinar nucleus receive projections from the superificial layer of the superior colliculus. Second, descending projections from cortical area 17 originate from layer V, while descending pathways from all other cortical areas in the visual field originate from layer VI. Third, the projections from area 17 and the superior colliculus onto the inferior pulvinar are retinotopically organized. The projections from the temporal lobe and areas 18 and 19 are at least topographically organized.

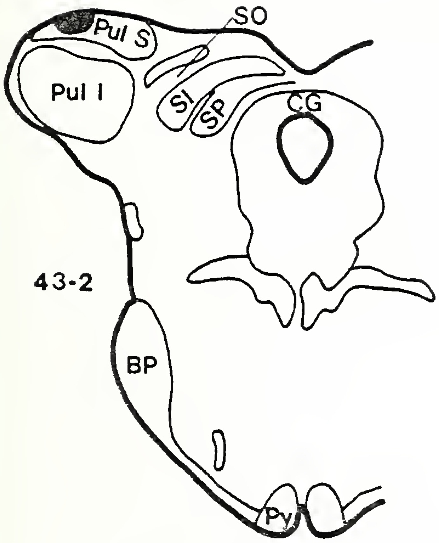
Part 2: Effects of Injecting HRP into the Superior Pulvinar Nucleus

Four experiments have been chosen to illustrate the effects of injecting HRP into the superior pulvinar nucleus.

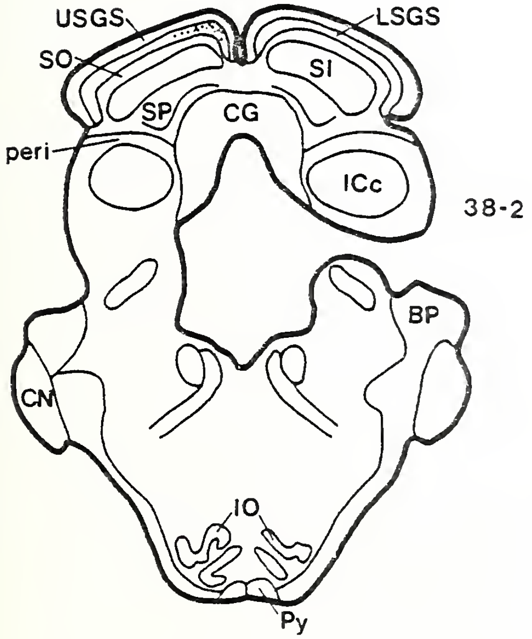
In Galago 1133R, a small amount of HRP was injected into the caudal pole of the superior pulvinar nucleus. The injection, illustrated in the upper left portion of figure 27, did not spread into the subadjacent inferior subdivision. This experiment makes two points. First, labeled cells were observed in the lower half of stratum griseum superficiale of the superior colliculus, indicating that the superior pulvinar is also a target of the superficial layers of the superior colliculus. As the figure indicates, the position of the labeled cells in the tectum follows the same organization observed after injections in the inferior pulvinar, i.e., lateral injections label neurons in the medial portion of the colliculus.

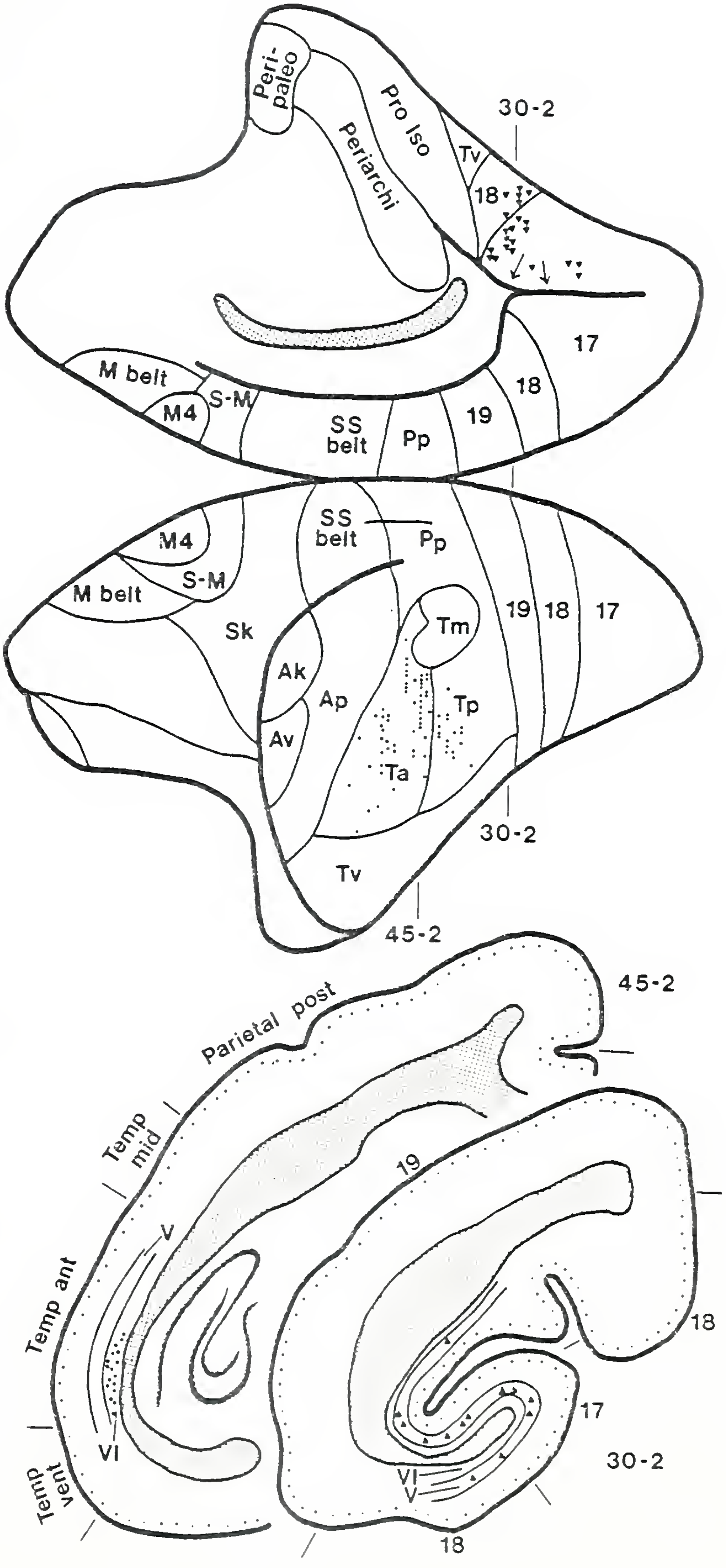
Figure 27. To show the distribution of labeled neurons in the brain stem and cortex after an injection of HRP into the superior pulvinar nucleus in *Galago* 1133R.

lateral



GALAGO 1133 R





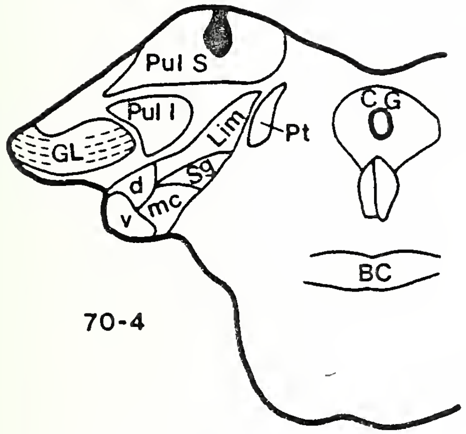
The second main point regards the distribution of labeled cells in the cortex. Again, two discontinuous patches of labeled cells are observed. One cluster of cells is located rostrally in areas Ta and Tp, and, as indicated by the figure, the labeled cells are located in layer VI. The second cluster of labeled cells is located in area 17 and, like the experiments in which HRP is injected into the inferior subdivision, all labeled cells are confined to layer V.

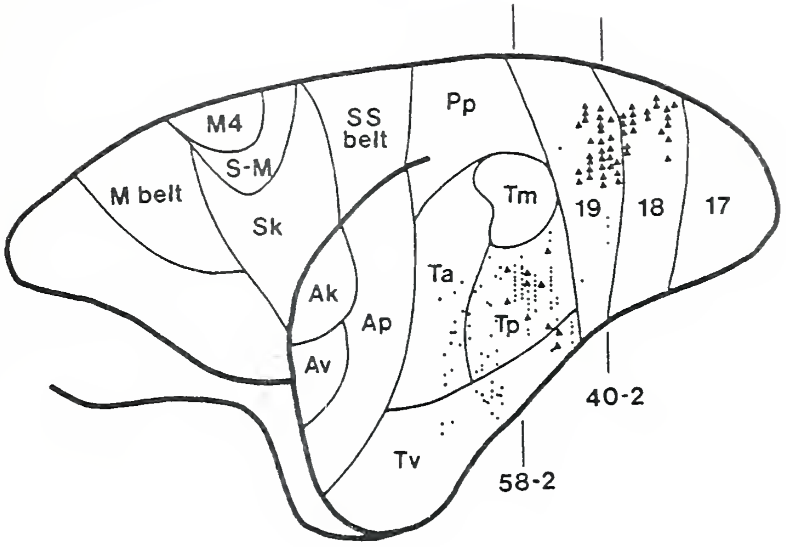
Of course, it may be argued that the area depicted in black in this experiment does not reflect the entire effective site of HRP uptake and that HRP did indeed spread over into the inferior pulvinar. The next experiment to be presented confirms the observation that the superior pulvinar receives a retinotopic projection from the superior colliculus.

In Galago 1306L, an electrophoretic injection of HRP was placed in the middle third of the superior subdivision. As figure 28 indicates, the injection is far removed from the common border with the inferior division. Even if the effective site of HRP uptake was twice as large as indicated, no HRP could have diffused into the inferior division. As section 65-2 indicates, once again labeled cells were observed in the lower half of stratum griseum superficiale of the superior colliculus. Due to the medial position of the injection, the labeled cells are located laterally in the lower half of stratum griseum superficiale.

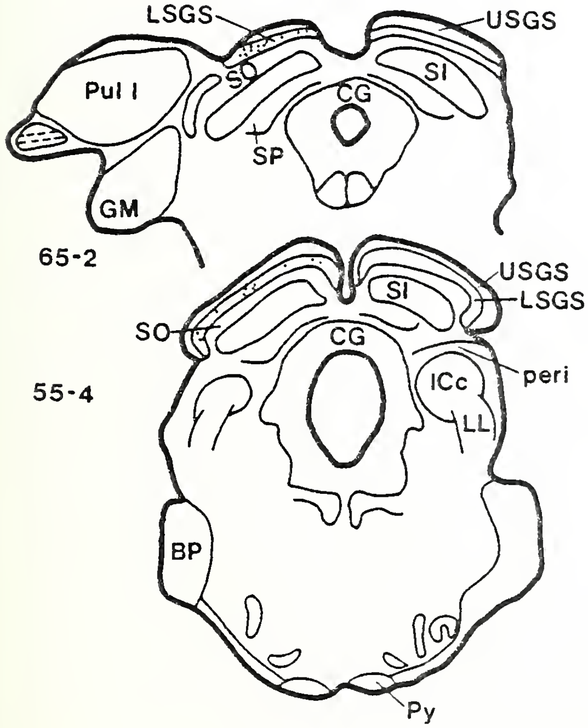
Turning now to a discussion of the labeled cells in the cortex, two points need to be emphasized. First, reflecting the more rostral

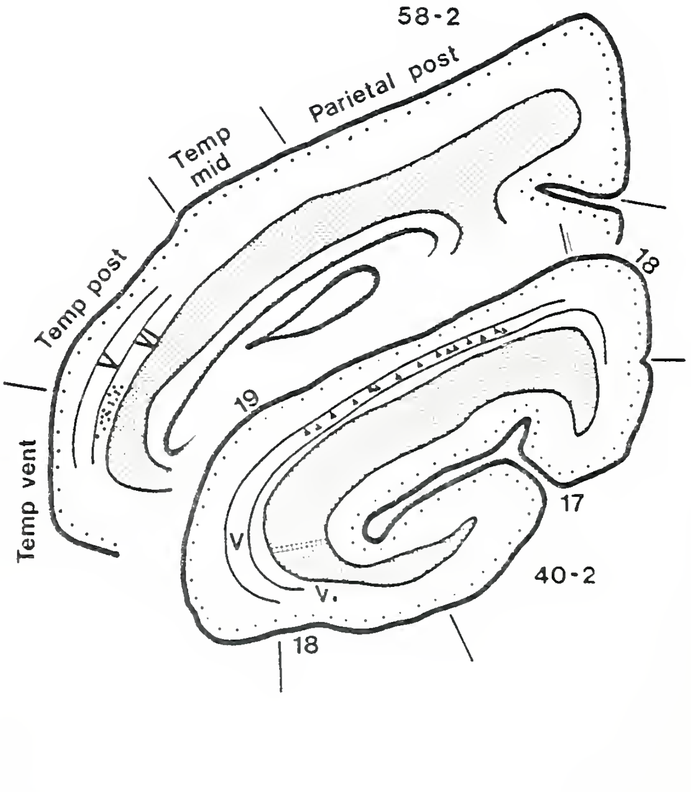
Figure 28. To show the distribution of labeled neurons in the brain stem and cortex after an injection of HRP into the superior pulvinar nucleus in Galago 1306L.





GALAGO 1306L



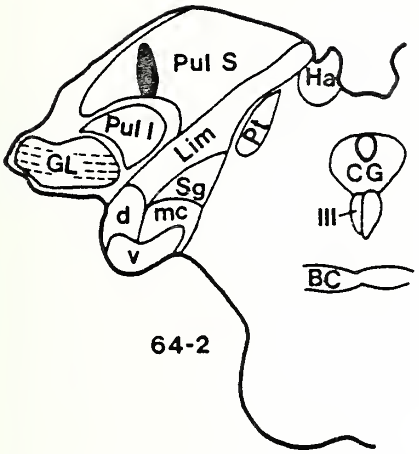


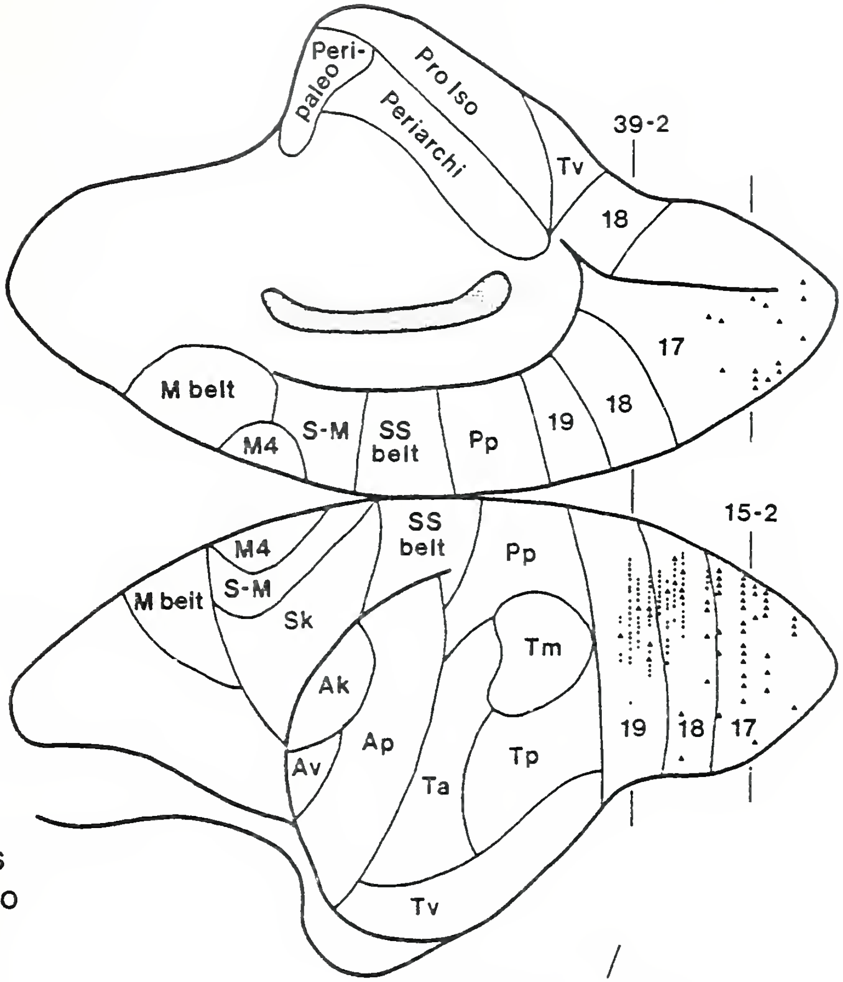
placements of the injection, the layer VI label in the temporal lobe is now concentrated in area Tp with a few scattered cells located in areas Ta and Tv. Second, although neurons in layer V were labeled following this injection, they were not located in area 17. Indeed, area 17 was free of labeled cells. Rather, the label in layer V is concentrated in areas 18 and 19. The significance of this projection remains obscure at this time.

In Galago 1397R, illustrated in figure 29, HRP was injected electrophoretically into the lateral half of the nucleus, at a level slightly rostral to the previous injection. In this experiment the injection extended to the ventral border of the superior pulvinar but did not extend beyond it. In the colliculus, labeled cells were again observed in the lower half of stratum griseum superficiale. Turning to the labeled cells in the cortex, the cluster of labeled cells has shifted such that all the layer VI HRP filled cells are now located in areas 18 and 19. Labeled cells were also present in layer V on the lateral surface of the striate cortex.

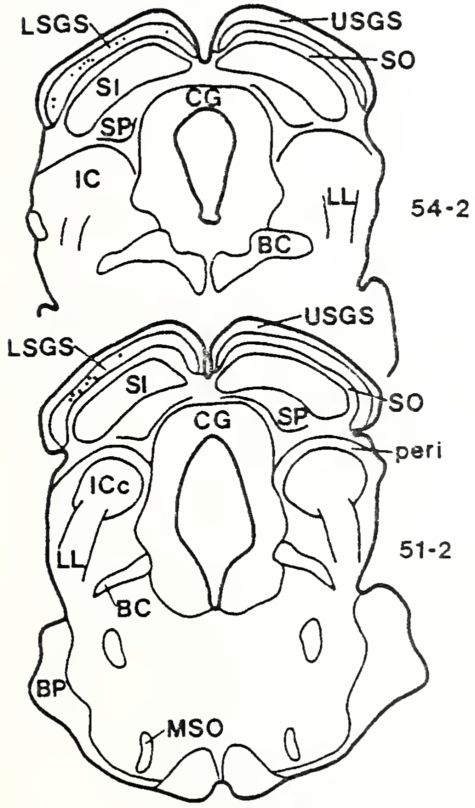
The final experiment to be presented is Galago 1391L in which an injection is placed in the rostral pole of the superior pulvinar. As figure 30 indicates, the injection is situated dorsomedially in the nucleus. Turning to an examination of the superior colliculus, labeled cells are observed in the extreme lateral portion of the lower half of stratum griseum superficiale. Thus, the entire superior pulvinar is the recipient of visual input from the superior colliculus.

Figure 29. To show the distribution of labeled neurons in the brain stem and cortex after an injection of HRP into the superior pulvinar nucleus in *Galago* 1397R.





GALAGO 1397 R



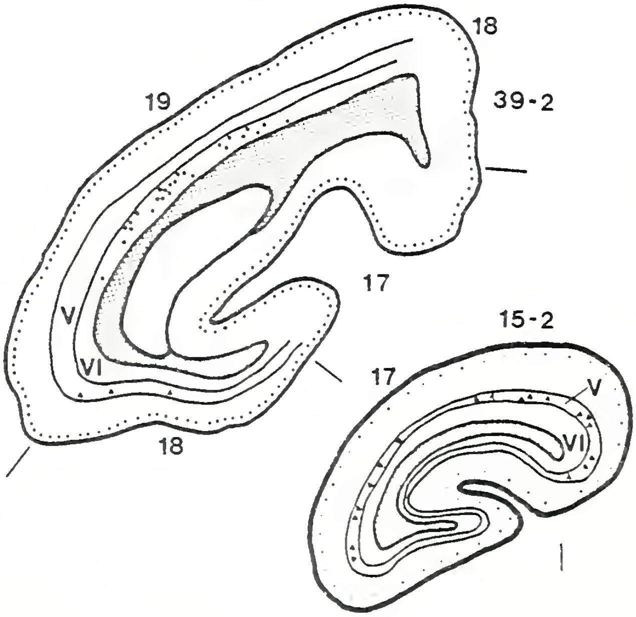
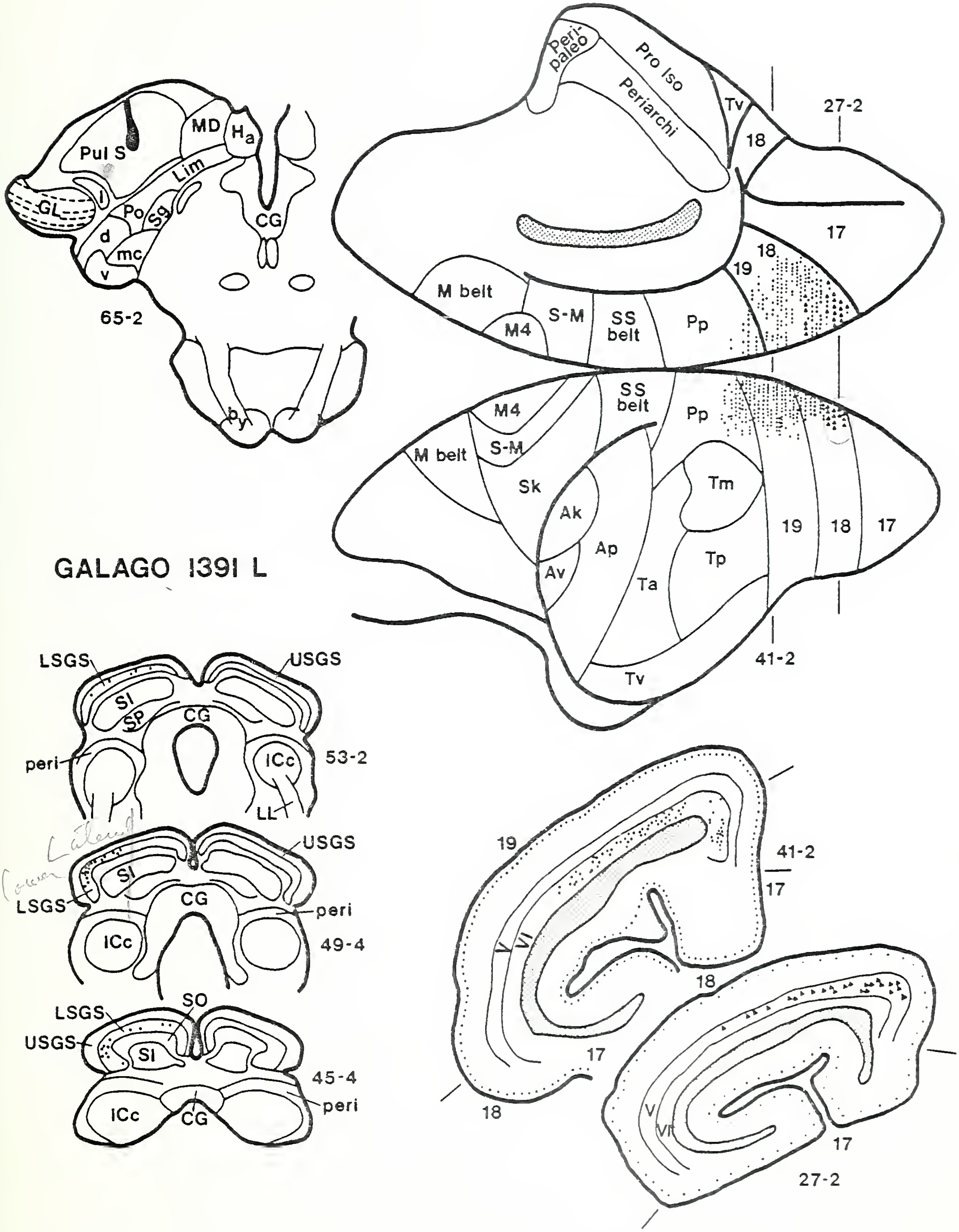


Figure 30. To show the distribution of labeled neurons in the brain stem and cortex after an injection of HRP into the superior pulvinar nucleus in *Galago* 1391L.

GALAGO 1391 L



In the cortex, the concentration of labeled layer VI neurons is again located in areas 18 and 19, but now the labeled cells are situated not only on the lateral surface, but also extend onto the medial wall. Thus, the topography of descending projections from the cortex outside area 17 to the superior pulvinar mimics that observed for projections to the inferior pulvinar. In other words, caudal injections label cells in area Ta, while rostral injections label cells in area 18. As observed in experiment 1306R, the labeled pyramidal cells in layer V were located not in area 17 but in area 18.

These four injections of HRP into the superior pulvinar make two points. First, the entire superior division receives a retinotopic projection from the lower half of stratum griseum superficiale of the superior colliculus. Second, the pulvinar superior receives descending projections originating from layers VI and V. The layer VI label which originates outside area 17 is topographically organized in a fashion similar to that observed for the inferior pulvinar nucleus.

III. Projections from the Cortex and Brainstem to the Superior Colliculus as Studied with the Horseradish Peroxidase Method

Introduction

In the previous section we showed that layer V of the striate cortex projects to the pulvinar nucleus. Previous experiments showed that this same cortical layer is also projecting to the tectum (Gilbert and Kelly,

'75; Hollander, '74; Jones et al., '76; Wise and Jones, '76). The next step seemed to be to study the cortical projections to the superior colliculus. First, it seemed important to determine whether the layer V pyramidal cells in area 17 which project to the pulvinar are the same neurons giving rise to descending projections to the superior colliculus. Second, the results of these experiments may contribute to an understanding of the functional significance of the laminar organization of the cortex and the closely related question of the meaning of architectonic subdivisions.

While the emphasis of these experiments was to examine the origin and distribution of HRP labeled cells in the cortex, these same experiments provided an opportunity to study ascending inputs to the tectum from the brain stem and retina. A systematic survey of the brain stem was made in every experiment, and these findings are included in this section. However, since the retina was not routinely processed, a description of the different types of ganglion cells labeled will not be included.

Placement of the HRP injections into superior colliculus was initially based on the distinction between superficial and deep layers previously described by lesion studies in the tree shrew and Galago (Casagrande et al., '72; Harting et al., '73a; Casagrande and Diamond, '74; Raczkowski et al., '76; Glendenning et al., '75). As the study progressed, it became evident that still another organization, not related

to architectonic distinctions, was present in the deeper layers, and some injections were placed along this dimension.

The results of these experiments will show first that layer V throughout most of the neocortex projects to the superior colliculus. From each of the three main sensory fields, auditory, somatic, and visual, fibers descend to the tectum. Second, each sensory field appears to have a separate target within the superior colliculus. These findings contribute to an understanding of the functional organization of the primate superior colliculus.

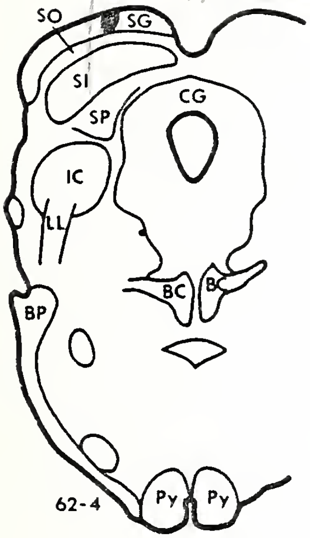
Experimental Results

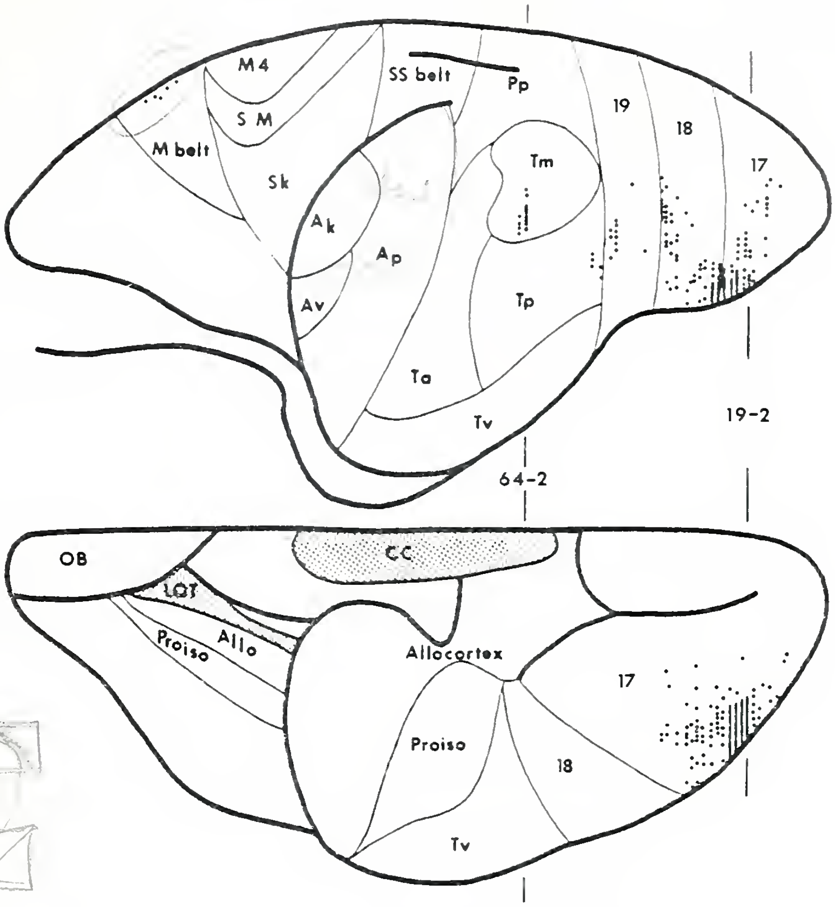
Part 1: Effects of Injecting the Superficial Layers

The result of injecting HRP into the stratum griseum superficiale is shown in experiment 1310L. The injection site, located in the middle third of the superior colliculus, is depicted in solid black in the upper left portion of figure 31; the diffusion of brown stain just encroaches on the border of stratum opticum. In the upper right portion of figure 31, two surface views of the *Galago* brain, lateral and ventral, illustrate the distribution of labeled cells in layer V of the neocortex. In the illustrations for this section, layer V labeled neurons are depicted as solid black dots. A heavy concentration of labeled cells is located in the lateroventral portion of area 17 on the border of area 18 and just across the border. Patches of labeled cells are also found in areas 19, the

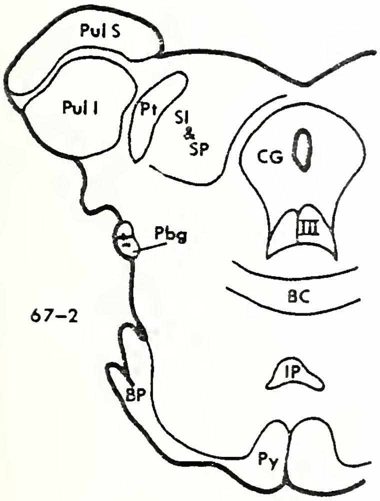
Figure 31. To show the distribution of labeled neurons in the brain stem and thalamus after an injection of HRP into the superior colliculus in *Galago* 1310L. The following convention applies to the next 8 line drawings. The locus of the injection is depicted in black in the upper left portion of the figure. Labeled neurons are depicted by solid dots in all the drawings. Labeled neurons in the brain stem are illustrated in the lower left portion of the figure. The distribution of labeled neurons in the cortex is shown in the upper right portion of the figure. Representative frontal sections to show the locations of labeled neurons are illustrated in the lower right portion of the figure.

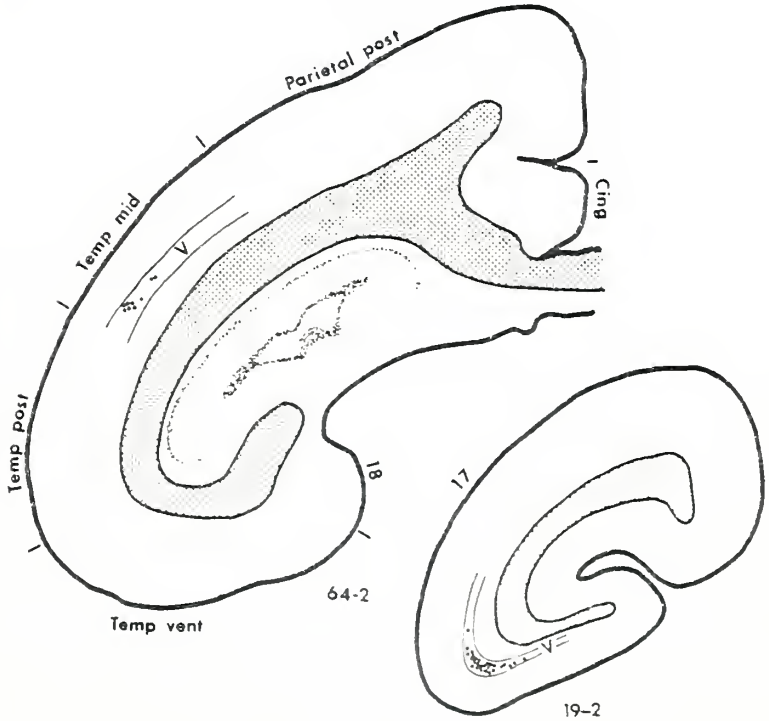
medial
upper level





GALAGO 1310L





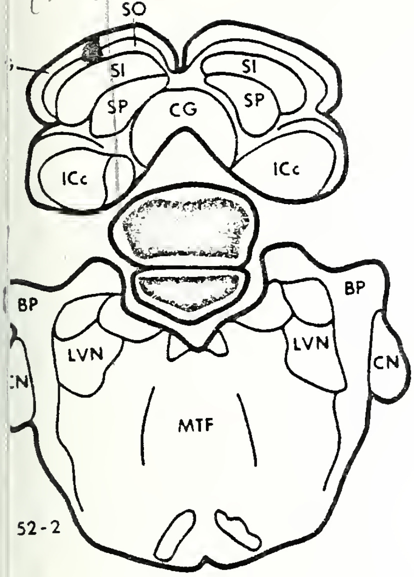
middle temporal cortex of the visual belt. No labeled cells were observed in the auditory field or in the somatic field other than portions of the motor belt which probably corresponds to area 8 or the frontal eye field in monkey (see Discussion). The frontal sections in the lower right of figure 31 makes the point that all of the labeled cells were confined to layer V. Even the largest neurons in the striate cortex, the so-called cells of Meynert, contain HRP granules.

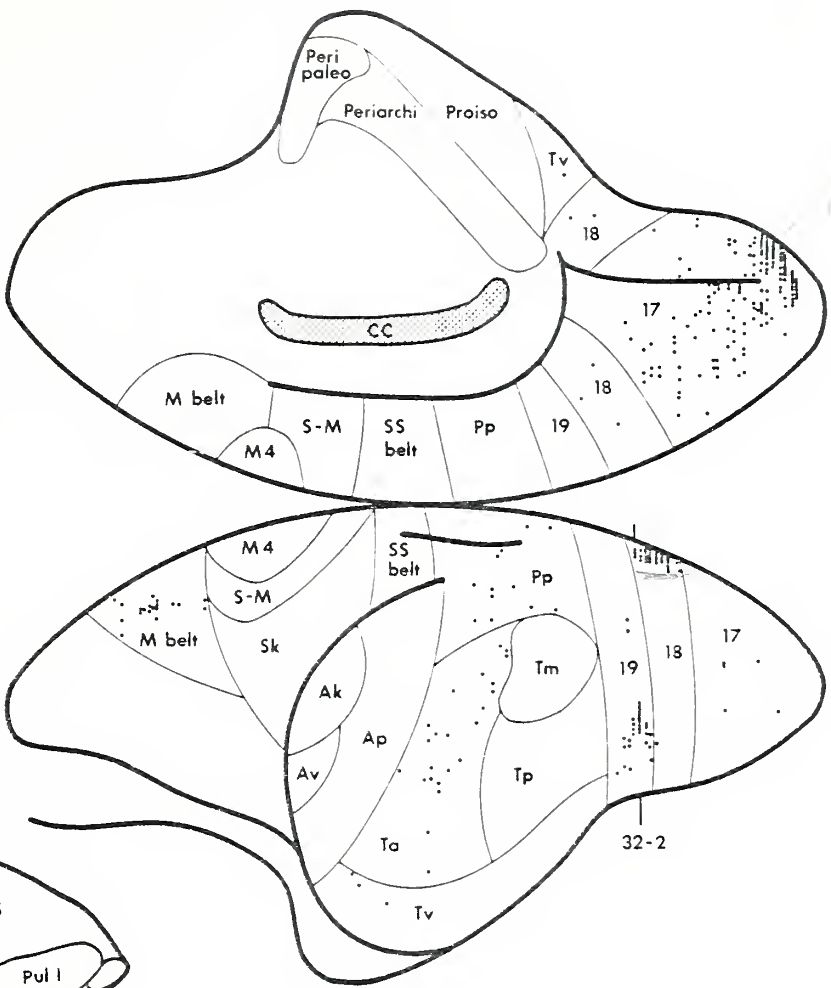
With regard to ascending brain stem inputs, the coronal section in the lower left of figure 31 makes the point that the parabigeminal nucleus projects to the superficial grey layers.

In Galago 1571L (figure 32), a small injection of HRP was made in the caudal portion of the superior colliculus. Although the aim of this experiment was to confine the HRP to the stratum griseum superficiale, we were unsuccessful and the brown stain also entered the stratum opticum. This experiment makes three points. First, it provides further information regarding the position of label in areas 17 and 18 relative to the injection site in the stratum griseum superficiale. In area 17, for example, the heaviest label in layer V is now situated at the caudal extent of the occipital pole behind the calcarine fissure. Second, this experiment indicates the effect of the brown stain entering the stratum opticum, i.e., the relatively heavy focus of labeled cells concentrated in area 19; as well as the scattered label located in the posterior parietal cortex. Scattered labeled cells were also observed

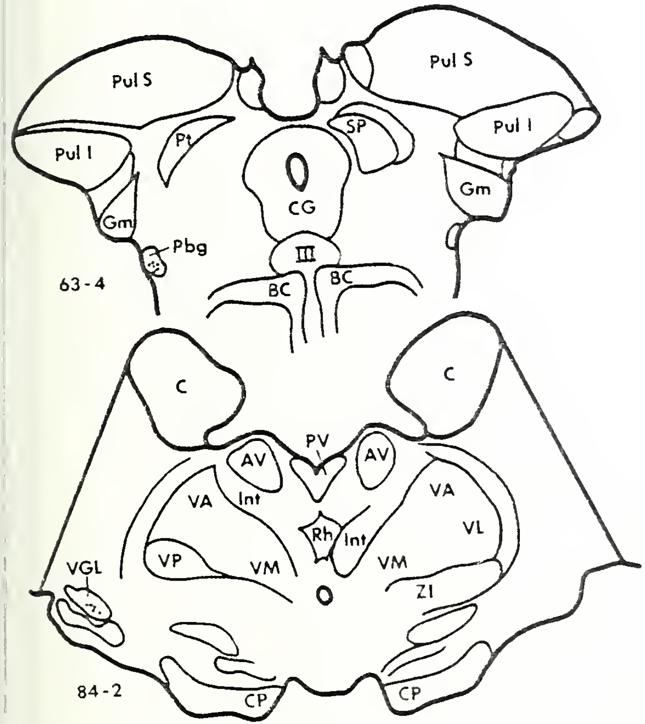
Figure 32. To show the distribution of labeled neurons in the brain stem and thalamus after an injection of HRP into the superior colliculus in *Galago* 1571L.

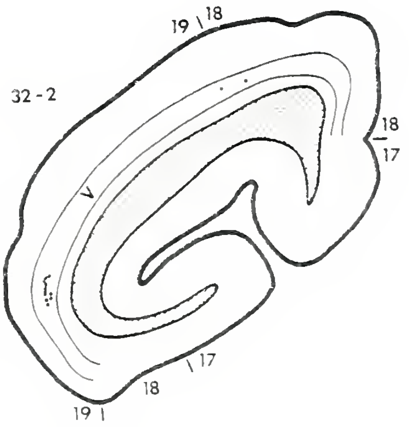
Coker





GALAGO 1571L





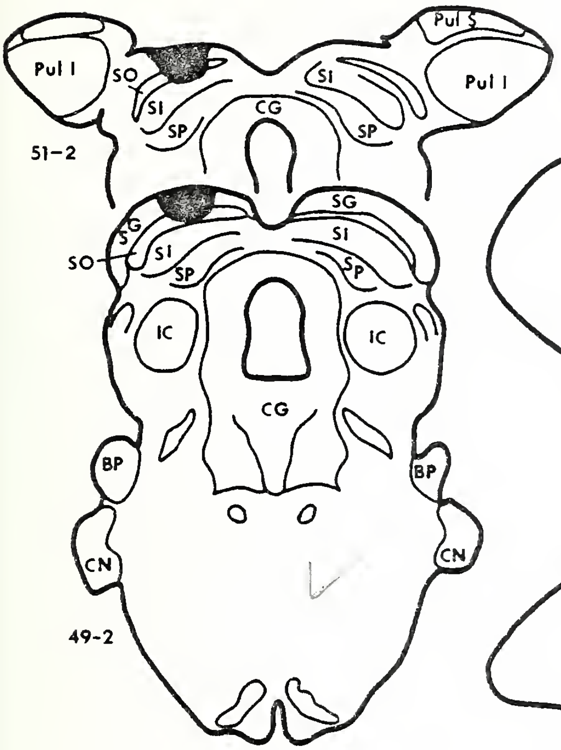
in the temporal cortex, areas Ta and Tv, and the motor belt.

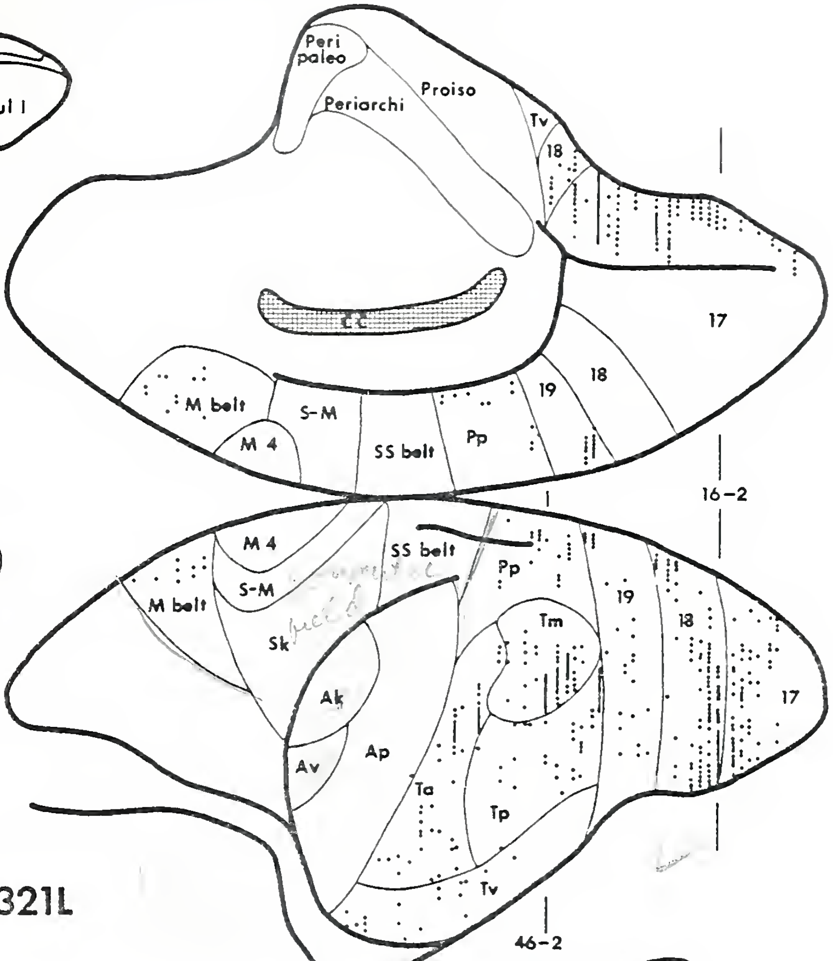
Third, this experiment makes the point that the upper layers of the superior colliculus (stratum griseum superficiale and stratum opticum) are exclusively visual inasmuch as no projection from the auditory and somatic fields was detected.

As the lower left portion of figure 32 indicates, labeled cells were again located in the parabigeminal nucleus; additional label was also observed in the ipsilateral ventral lateral geniculate body. This injection also labeled cells in stratum opticum and stratum intermediale of the contralateral colliculus.

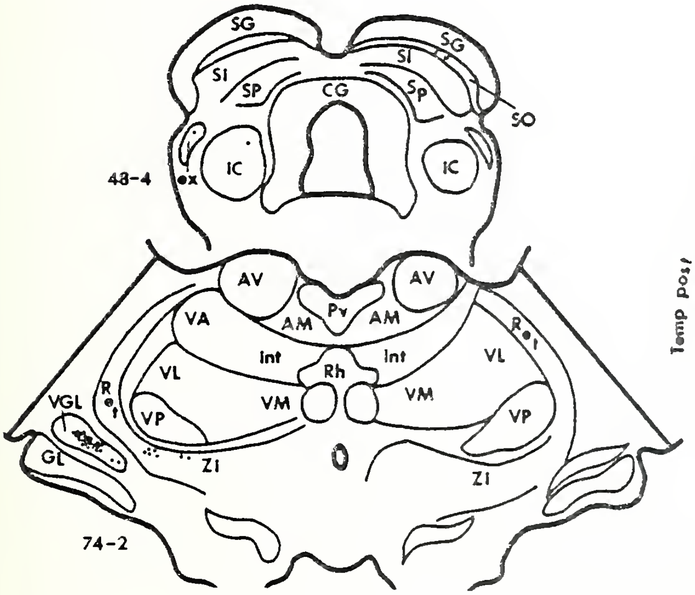
Figure 33, illustrating experiment 1321L, summarizes the effect of a large injection of the rostral colliculus. The effective site of HRP uptake appears confined to the stratum griseum superficiale and stratum opticum, although at more rostral levels the brown stain appears to have diffused into the upper portion of the stratum intermediale. Corresponding to the large size of the injection, as well as the encroachment into the intermediate layers (see below), many more labeled cells are present in layer V of the cortex than were seen in the previous two experiments. The labeled cells are concentrated along the 17-18 border as in experiment 1310L, but now labeled cells are more numerous and more widely distributed in the visual field. The main point of this case is that this single injection labeled the entire visual field. With the notable exception of the projection arising from the motor belt, no other areas

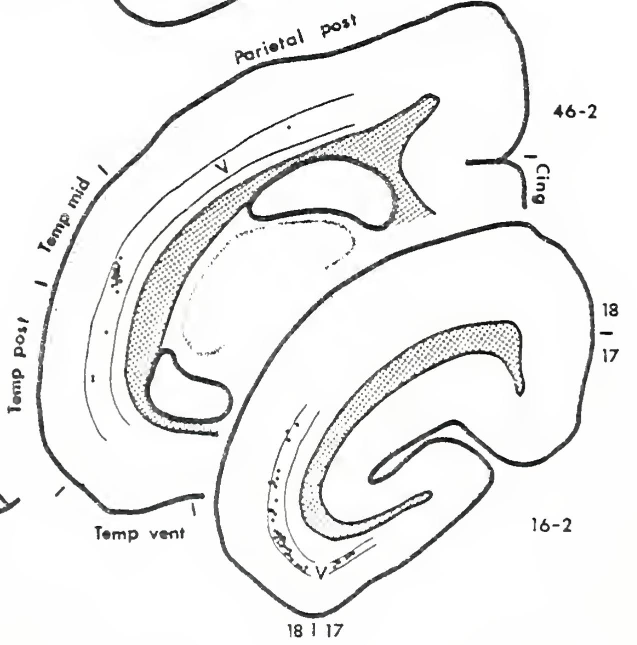
Figure 33. To show the distribution of labeled neurons in the brain stem and thalamus after an injection of HRP into the superior colliculus in Galago 1321L.





GALAGO 1321L





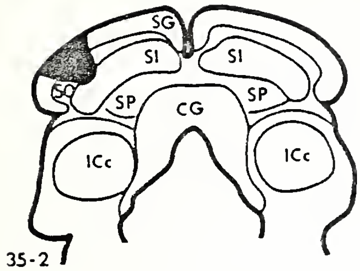
of the cortex contained labeled cells.

In the brain stem, label is located in the same visually related structures as in the previous experiment. In addition, labeled cells are also observed in two non-visual nuclei, the inferior colliculus and zona incerta.

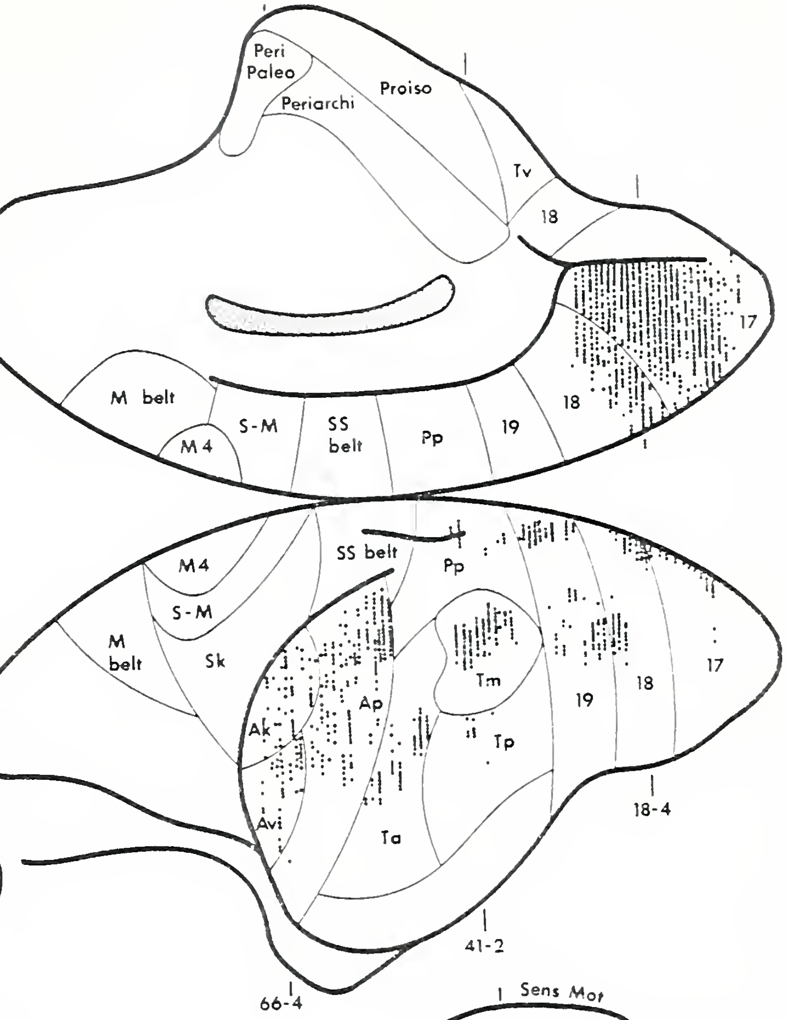
The final experiment in this section, *Galago* 1141L, illustrated in figure 34, shows the effect of injecting the lateral portion of the superior colliculus with HRP. The aim of this experiment was to confine the HRP to the stratum opticum; however, as indicated in the upper left of figure 34, the brown stain extended dorsally into the stratum griseum superficiale and ventrally into the stratum intermediale. The injection in this case was rather large, and this is reflected in the number and distribution of labeled cells in layer V of the visual and auditory fields.

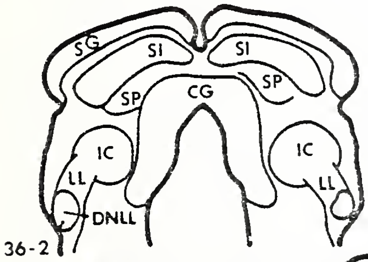
Turning to the pattern of cortical labeled cells, a concentration is located on the medial surface of area 17 above the calcarine fissure and extending over the dorsal surface onto the lateral aspect of the striate area. This portion of area 17 is located in the representation of the lower visual field, corresponding to the injection site in the colliculus, which also is located in the representation of the lower visual field. An intense focus of label is also located in area 18. Confirming the results of previous experiments, injecting the optic layer produces dense patches of labeled cells in layer V of area 19 and the visual portion of the temporal lobe, especially areas Tm and Ta. The position of the labeled

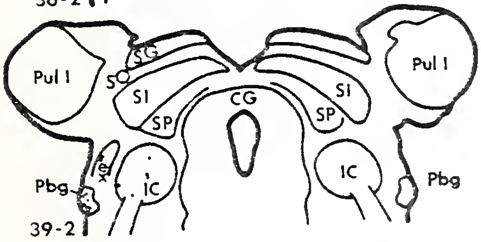
Figure 34. To show the distribution of labeled neurons in the brain stem and thalamus after an injection of HRP into the superior colliculus in Galago 1141L.

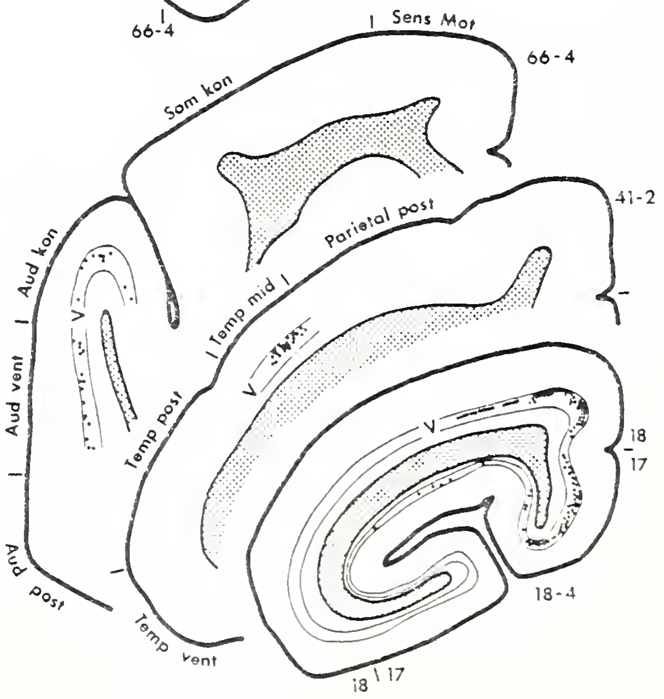


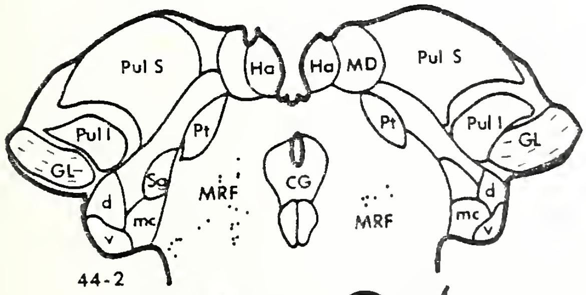
GALAGO 1141L

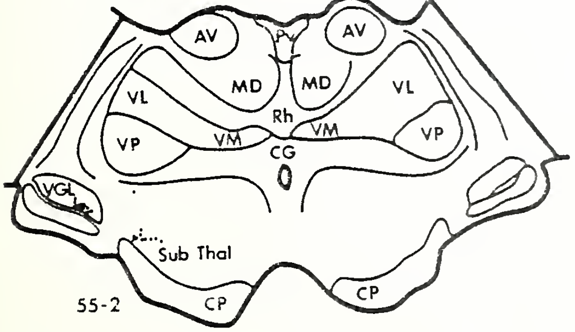












cells in area Tm suggests that this area projects topographically onto the superior colliculus. A few scattered labeled cells are also located in the posterior parietal cortex.

In contrast to the previous experiments presented in this section, an extensive population of labeled cells was located outside the visual field in the auditory portion of the temporal lobe. This projection will be described in detail in the next section. Suffice it to say, at this time, that the labeled cells in the auditory field can be attributed to the brown stain extending into the caudal portion of stratum intermediale.

A variety of brain stem nuclei contained labeled cells, and this observation is illustrated in the lower left of figure 34. Two of these nuclei, the parabigeminal nucleus and the ventral lateral geniculate, have already been shown to project to the superficial layers. The remaining nuclei containing labeled cells will be discussed in the next section. Summing these four experiments, the whole visual field, but no areas outside the visual field, project to the superficial layers of the superior colliculus. The notable exception is that the motor belt, which probably corresponds to the frontal eye fields, contains labeled cells. With regard to topography, it would appear that the rostral superficial layers are especially connected with the 17-18 border.

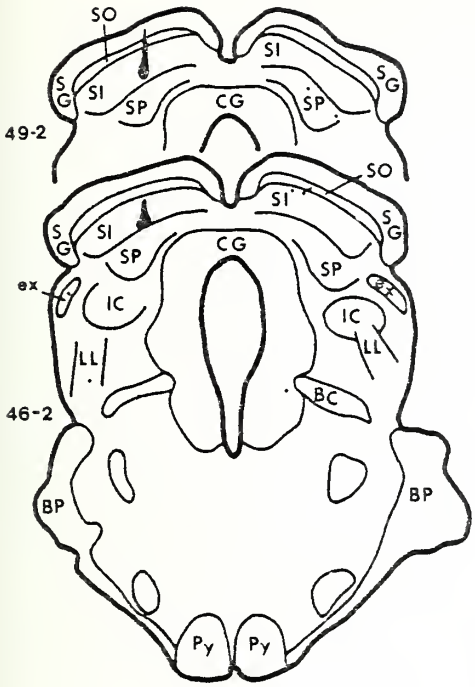
Part 2: Effects of Injecting HRP into the Deeper Layers

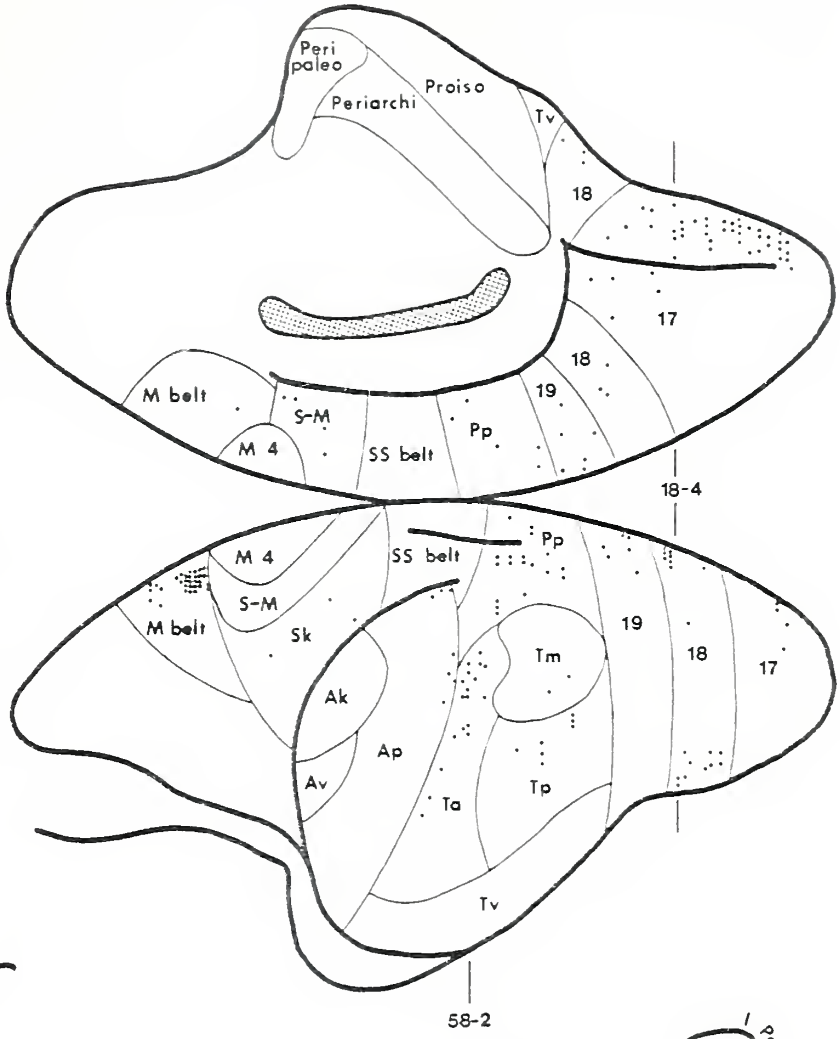
The superficial layers (stratum griseum superficiale and stratum

opticum) have been shown to be exclusively visual, as judged by the pattern of labeled cells in the cortex and brain stem. The experiments we will present in this section will show that injecting the deeper layers produces labeled cells in all three sensory fields, but the patterns of distribution produced by injecting different portions of these deeper layers were quite distinct. In each pattern, one sensory field contains most of the labeled cells. At the same time, the total cortex containing labeled cells was constant, and there was considerable overlap. Thus, in 5 of 6 experiments to be presented, labeled cells were located in the posterior parietal cortex.

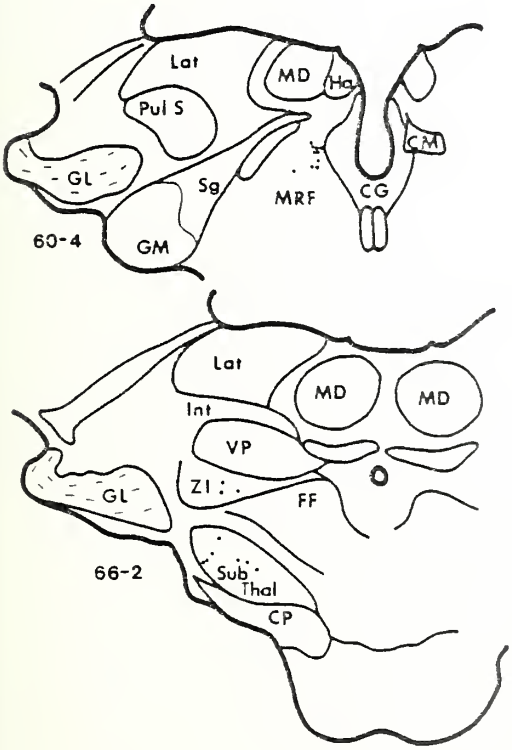
In *Galago* 1293L (see figure 35), a small amount of HRP was injected into the rostral portion of the stratum intermediale. While the main focus of the injection is in the upper half of the stratum intermediale, some HRP appears along the electrode track in the superficial layers. The main point of this experiment is to demonstrate that injections in the rostral portion of the stratum intermediale led to labeling of cells mainly in the visual field. However, the distribution of labeled cells *within* the visual field is quite different from that seen after injecting the superficial layers. Most of the labeled cells are concentrated in the temporal areas of the visual field with only scattered labeled cells located in areas 17, 18, and 19. Two additional patches of labeled cells are located in the posterior parietal cortex and the motor belt region. Finally, one or two neurons were present in the somatic field

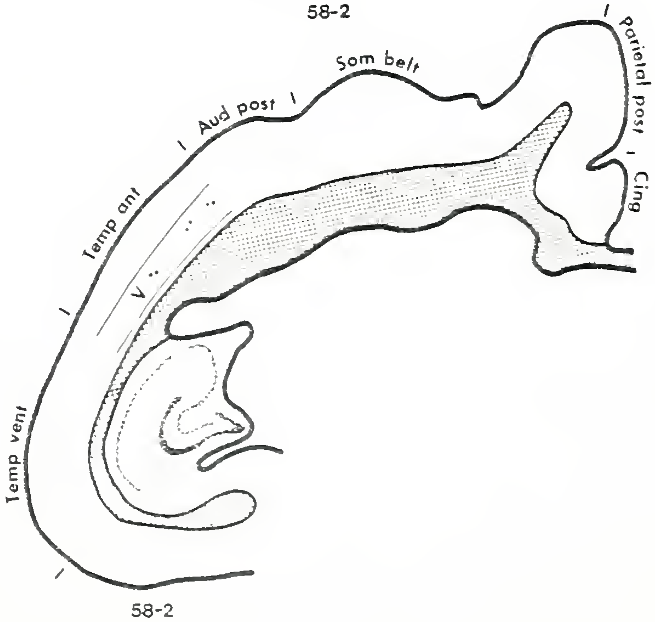
Figure 35. To show the distribution of labeled neurons in the brain stem and thalamus after an injection of HRP into the superior colliculus in Galago 1293L.





GALAGO 1293L



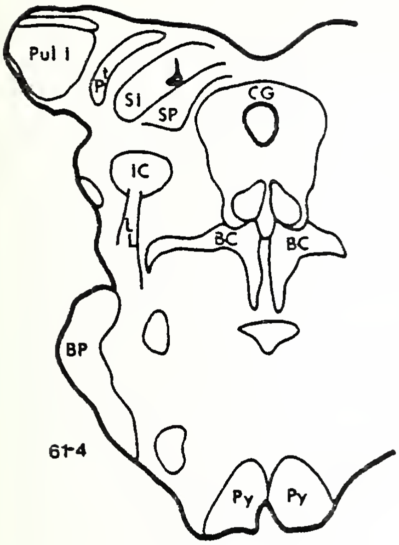


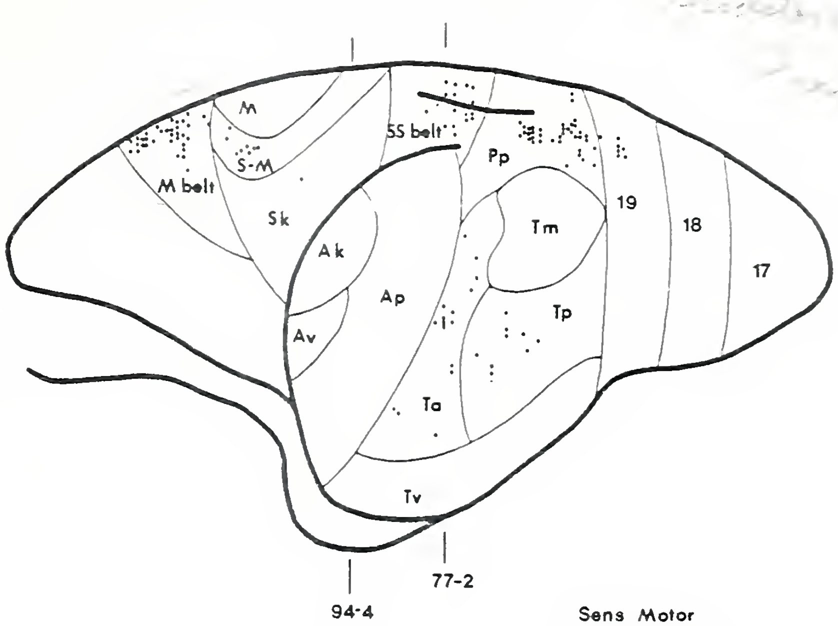
The left portion of figure 35 also makes the point that visual and non-visual related brain stem nuclei project to the deeper layers. The external nucleus of the inferior colliculus and the dorsal nucleus of the lateral lemniscus, known auditory relay nuclei, contained a few labeled cells as did zona incerta, which is related to the somatosensory path. Visual inputs are observed arising from the deep layers of the contralateral superior colliculus. Additional label is contained in the mesencephalic reticular formation and subthalamus.

In Galago 1294L, another injection was placed rostrally in the stratum intermediale. As figure 36 illustrates, the brown stain extended into the deepest portions of the stratum intermediale and no HRP was evident in the superficial layers. The labeled cells are most concentrated within the somatic field, in the somatic and motor belts. In the visual field, the distribution of label is confined to areas Ta and Tp and the upper part of 19. Areas 17, 18, and Tm are spared. As in the previous experiment, a dense focus of label is located in the posterior parietal cortex. It is important to note that no label is contained within the auditory field.

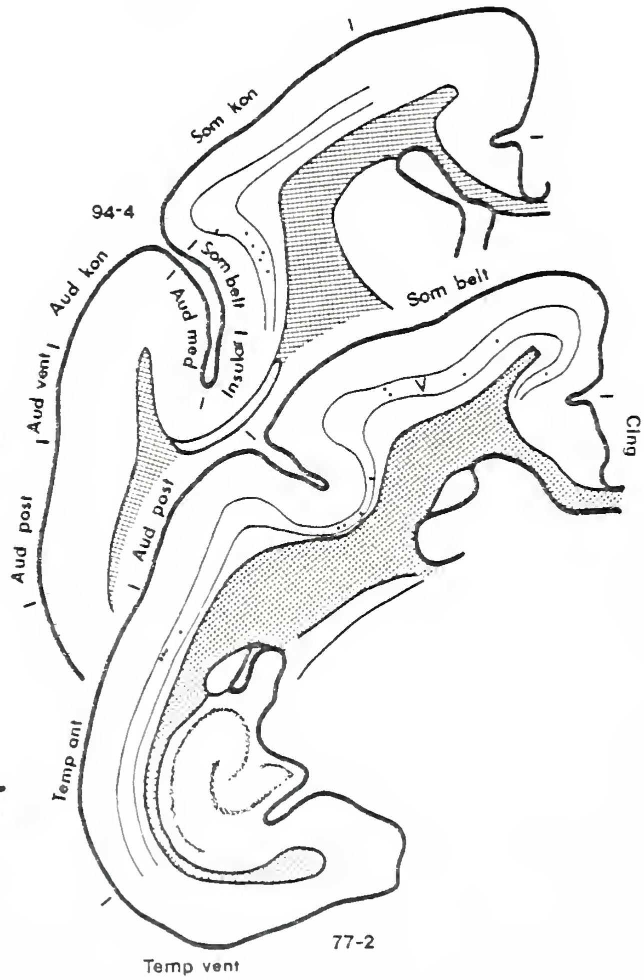
Paralleling the descending cortical projections, visual and somatic related brain stem nuclei contained labeled cells. In this experiment, HRP positive neurons were observed in stratum opticum and stratum intermediale of the contralateral superior colliculus, in zona incerta and the subthalamus.

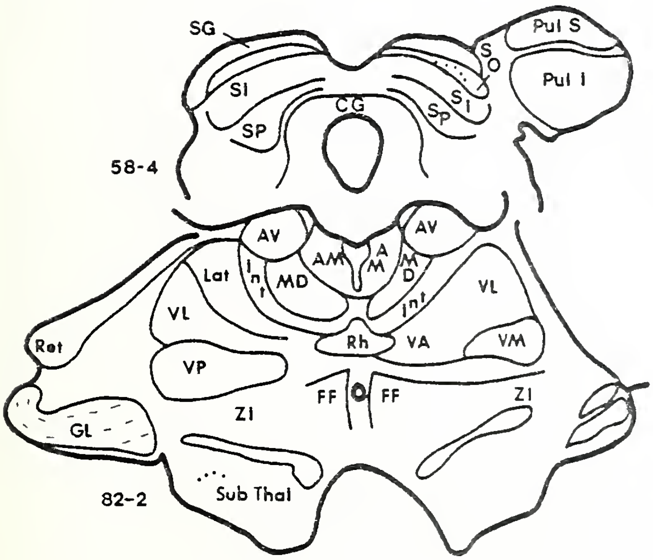
Figure 36. To show the distribution of labeled neurons in the brain stem and thalamus after an injection of HRP into the superior colliculus in Galago 1294L.





GALAGO 1294 L



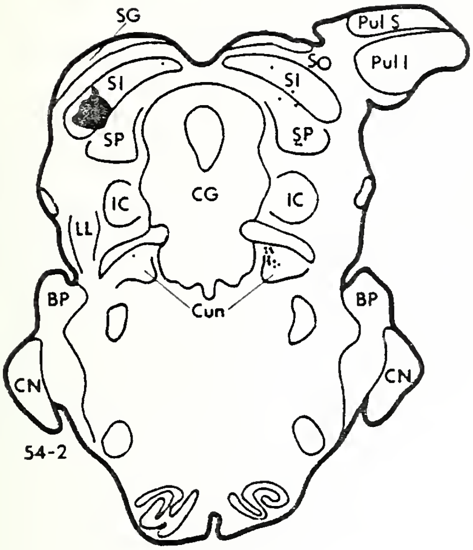


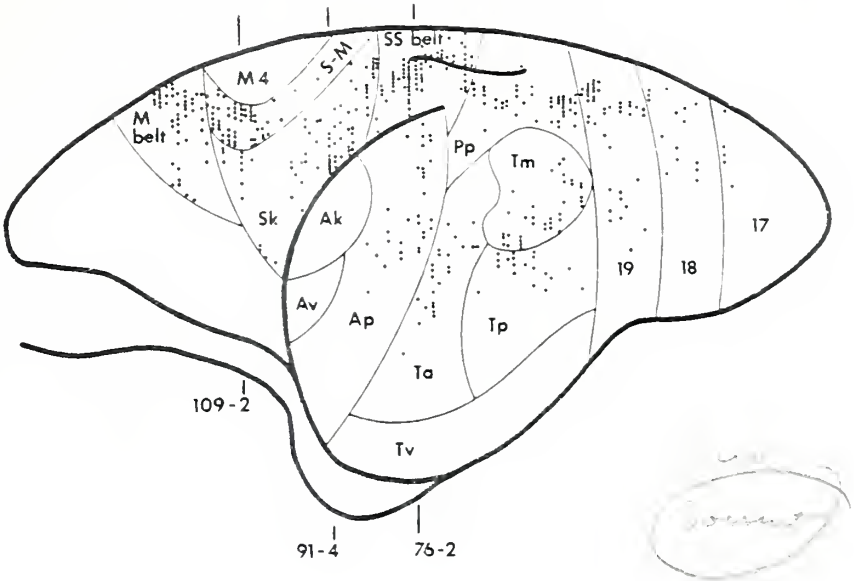
In Galago 1541L, a large injection of HRP was placed laterally in the stratum intermediale with the result that a concentration of labeled cells is located in each subdivision of the somatic field, except Motor 4 (see figure 37). Scattered patches of label are also evident in the visual and auditory fields.

As in the previous experiments in this section, labeled cells were observed in the contralateral superior colliculus, in stratum opticum, stratum intermediale, and stratum profundum. Labeled cells were also observed ipsilaterally in zona incerta and the subthalamus. At least two brain stem structures project bilaterally to a portion of the colliculus. In the mesencephalic reticular formation, a greater number of labeled cells were located ipsilateral to the injection, while in the cuneiform nucleus the labeled cells were located primarily contralateral to the injection. Finally, a few labeled cells were contained in the magnocellular tegmental field.

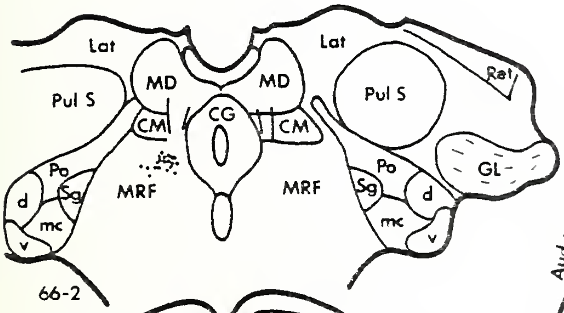
The final experiments to be presented in this section demonstrate that portions of the intermediate layers are the recipients of a prominent projection from the auditory field. In the first case, 1128L, the injection is now situated in the caudal aspect of the stratum intermediale and, in contrast to the patterns already presented, the vast majority of neurons are located in the auditory field (see figure 38). The heaviest label in this cortex is seen in Ap and the labeled cells are the largest in the auditory field. Additional label is observed in the posterior parietal and

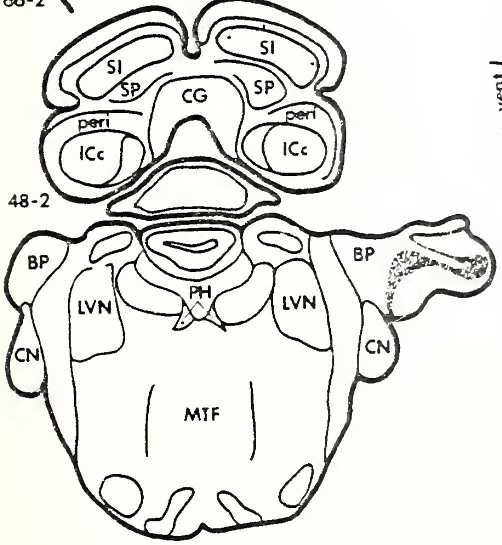
Figure 37. To show the distribution of labeled neurons in the brain stem and thalamus after an injection of HRP into the superior colliculus in Galago 1541L.





GALAGO 1541L





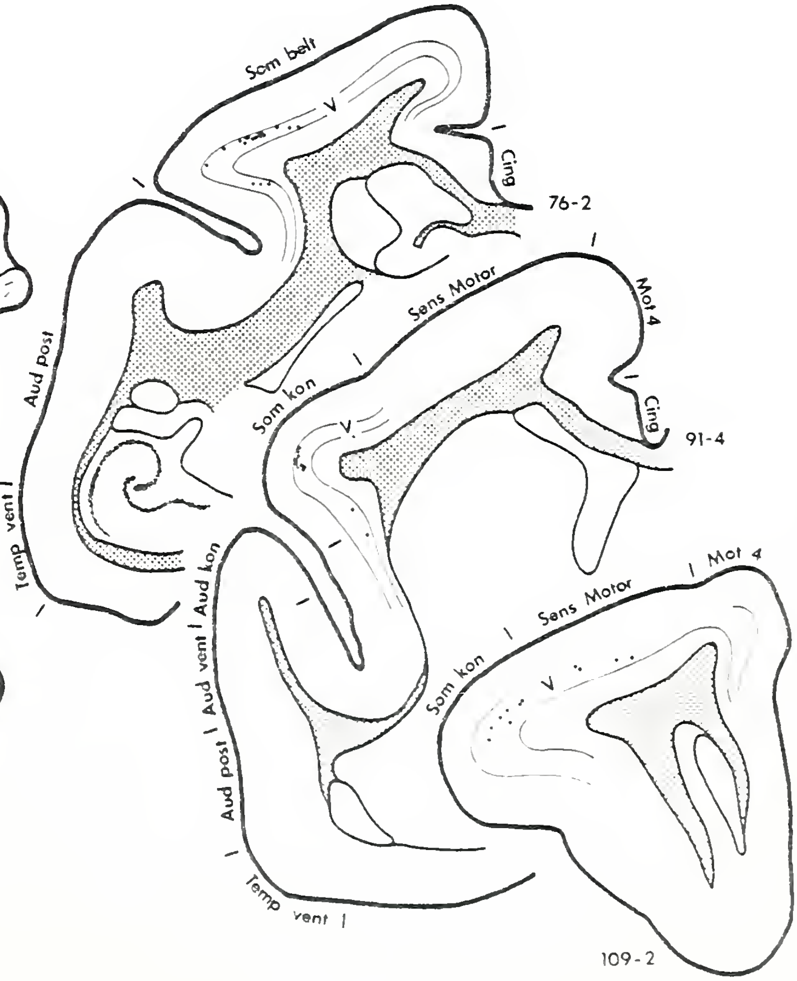
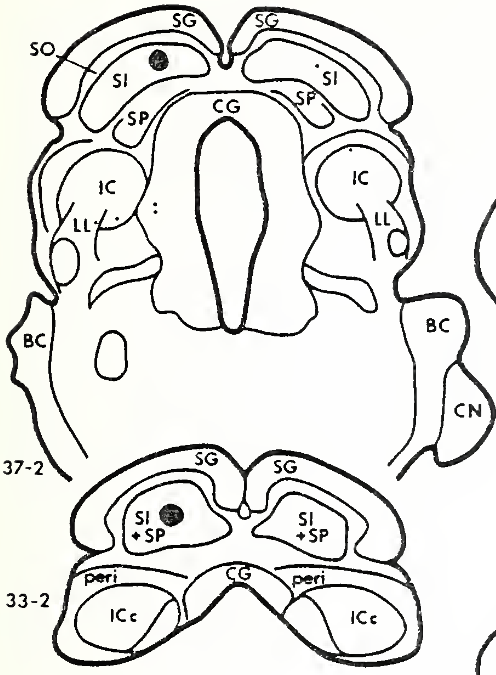
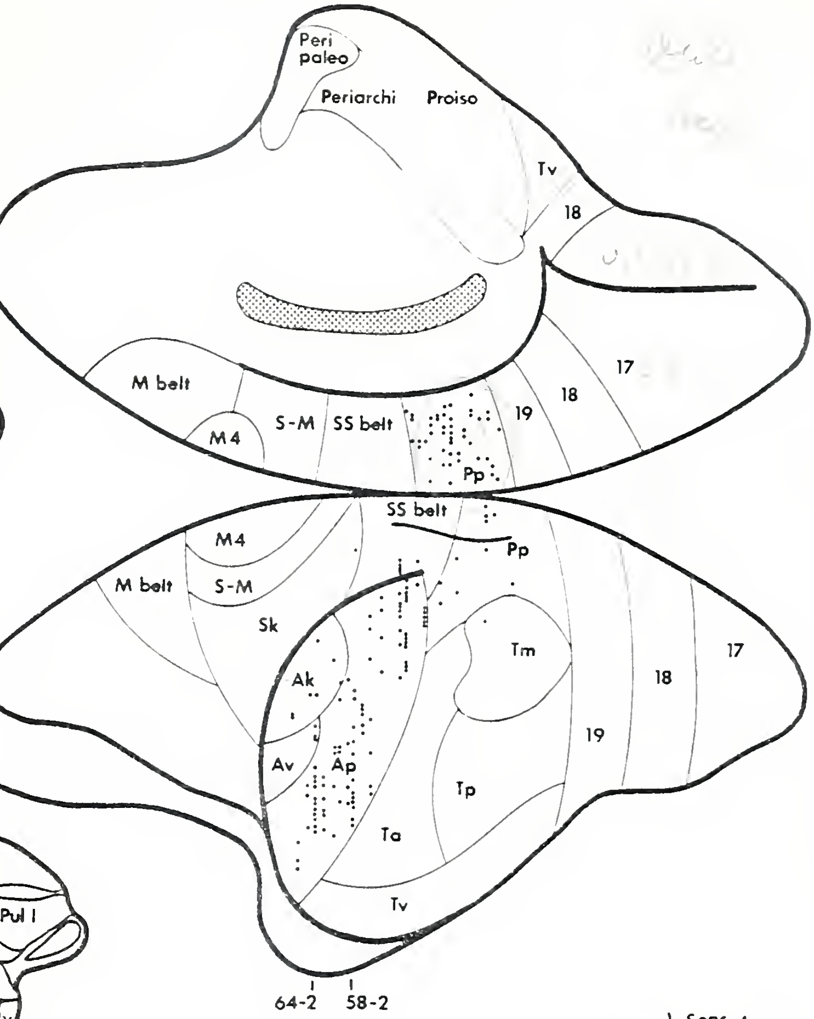
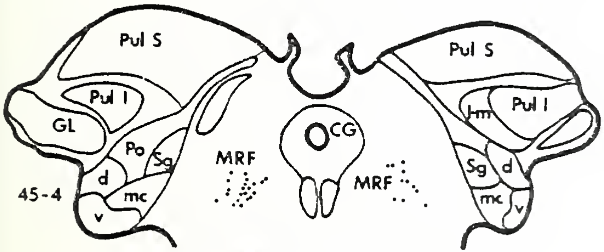


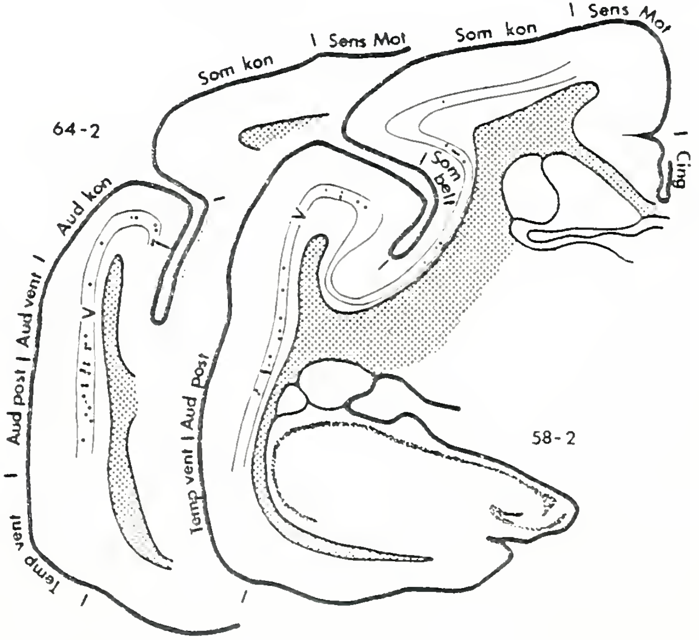
Figure 38. To show the distribution of labeled neurons in the brain stem and thalamus after an injection of HRP into the superior colliculus in Galago 1128L.

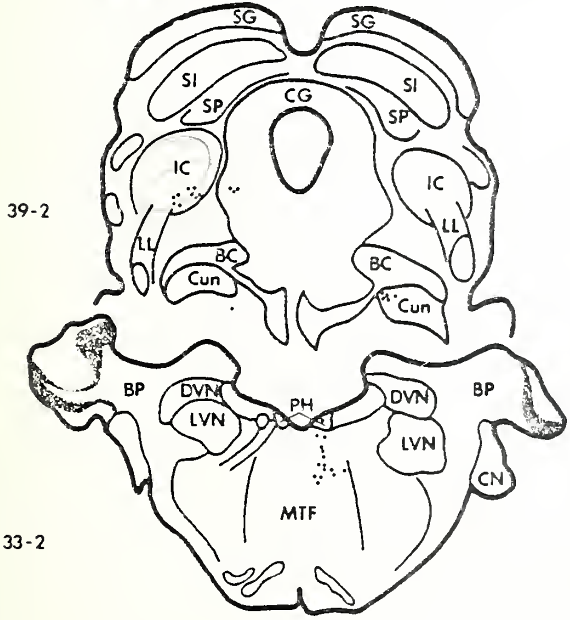




GALAGO 1128L







somatic belt cortices. No labeled cells were located in the visual field.

In the brain stem, a different pattern of label is also observed. Labeled cells are located in the contralateral mesencephalic reticular formation in the lower brain stem. At midbrain levels, label is observed contralaterally in the cuneiform nucleus, the contralateral superior colliculus, and bilaterally in the inferior colliculus. More rostrally, labeled cells are located bilaterally in the mesencephalic reticular formation.

To support the observations that the caudal portion of the stratum intermediale is especially connected with the auditory path, we return to experiment 1141L (figure 34) which contains an injection of HRP restricted to the caudal and lateral portion of the stratum griseum superficiale and the stratum intermediale. The distribution of labeled cells in the visual field have previously been described, and we will concern ourselves now only with the projection from the auditory cortex. The heaviest concentration of labeled cells in the auditory field, again, is located in Ap, the cortical area receiving ascending projections from the dorsal division of the medial geniculate body. Additional projections originate in layer V of the auditory konio and ventral areas of the auditory field. These areas of cortex are the targets of the ventral and caudal subdivisions of the medial geniculate body, respectively.

In the brain stem, auditory relay nuclei containing labeled cells include subdivisions of the inferior colliculus and the dorsal nucleus of the lateral lemniscus. Other structures projecting to this portion of the

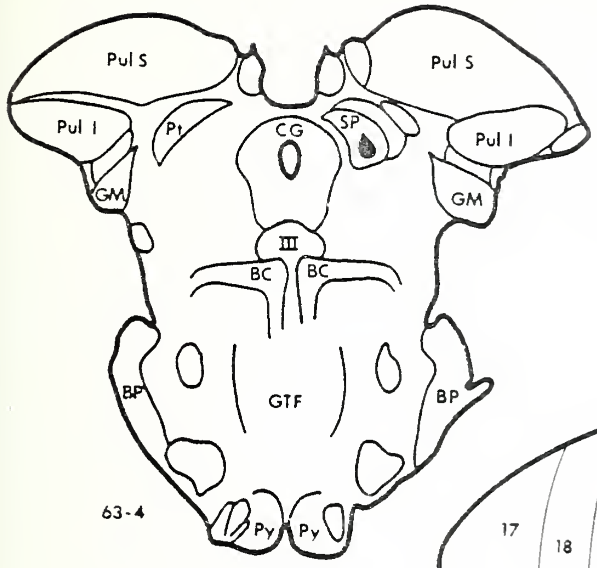
superior colliculus, not mentioned previously, include the subthalamus and mesencephalic reticular formation.

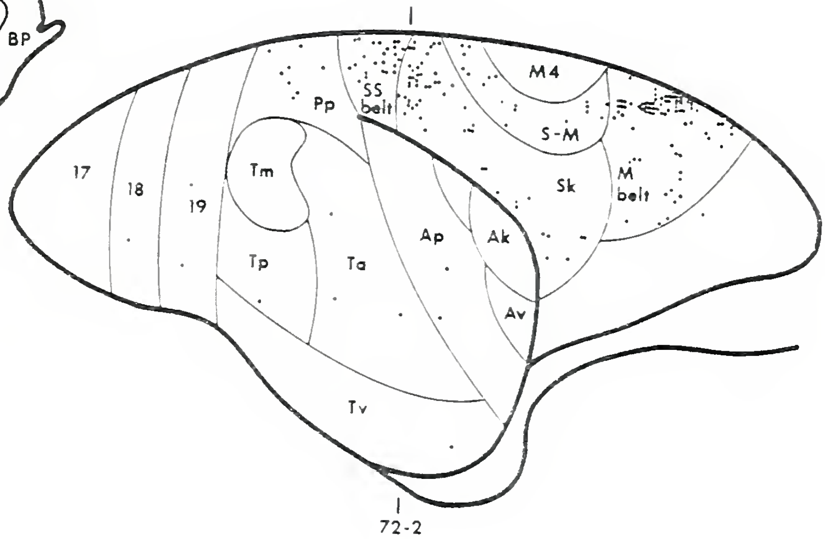
Galago 1571R, illustrated in figure 39, is the only experiment in which we were successful in restricting the HRP to the stratum profundum. This experiment makes the point that only the somatic field contains labeled cells. Every subdivision of the somatic field, except Motor 4, is involved in this projection. A few scattered cells are located throughout the visual field. In the brain stem, label was seen in the ipsilateral zona incerta as well as in the stratum profundum of the contralateral colliculus.

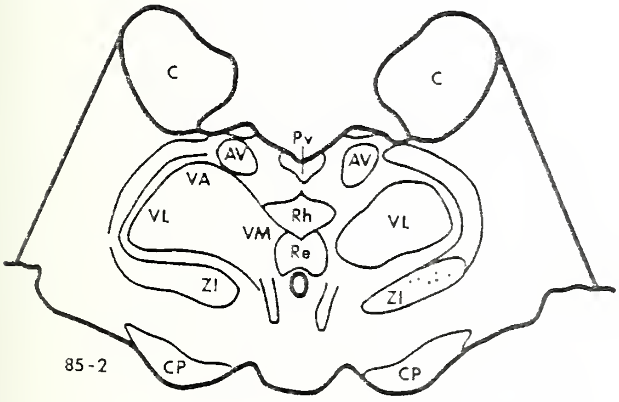
It would appear from a review of these six experiments that the deeper layers are subdivided into regions, each of which is especially connected with one particular sensory field. Thus, after injections involving the rostral portion of the stratum intermediale, labeled cells are concentrated in the visual field. When the site of injection shifts laterally, the greatest concentration of labeled cells is contained within the somatic field. Only when the injection involves the caudal portion of the stratum intermediale does the auditory field contain a substantial number of labeled cells. Finally, after an injection confined to the stratum profundum, labeled cells were restricted to the somatic field.

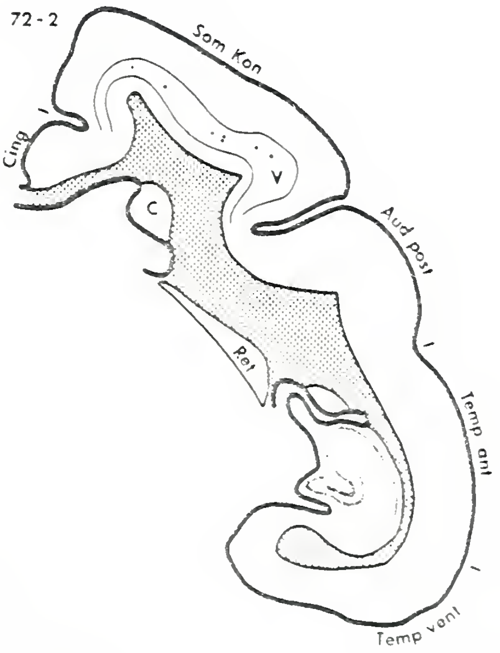
Figure 39. To show the distribution of labeled neurons in the brain stem and thalamus after an injection of HRP into the superior colliculus in Galago 1571R.

GALAGO 1571R









IV. Projections from the Visual Cortex to the Thalamus and Superior Colliculus Studied with the Autoradiographic Method

Introduction

In the first section, the projections of the pulvinar were studied by placing small HRP injections into the cortex. This method showed all of the thalamic cells projecting to a small restricted cortical locus. In the second section, descending reciprocal projections from the cortex to the pulvinar were revealed by injecting HRP into the pulvinar. But this technique does not reveal precisely the topography of the reciprocity because all of the cortex projecting to a single thalamic locus is revealed while what is necessary is to depict all of the thalamic areas which receive descending projections from a restricted cortical locus.

In this final section, we examine whether the connections between the pulvinar and the cortex are reciprocal by injecting tritiated amino acids into each subdivision of the visual field and then examining the patterns of silver grains over the thalamus. Furthermore, since it has been shown earlier that layer V of area 17 projects to the pulvinar and tectum, these experiments, especially the area 17 injection, can address the issue as to whether the HRP entered axons passing through the pulvinar nucleus en route to the tectum. The results will demonstrate reciprocally organized interconnections between the pulvinar and the various cortical areas of the visual field and that, indeed, there is a pathway from the striate cortex to the pulvinar nucleus. Finally, these

experiments will be shown to support the functional organization of the superior colliculus as revealed in the previous chapter with the HRP method.

Experimental Results

From 24 cases, 7 experiments have been selected to illustrate the pattern of descending corticothalamic and corticotectal projections from each of the cytoarchitectonic areas comprising the visual field of Galago. In each experiment, the pattern of termination in the midbrain will be described first, followed by a description of the cortical projections to the pulvinar complex and dorsal lateral geniculate body. Transport to other brain stem nuclei and basal ganglia will not be described.

Injection of area 17. Four injections of tritiated amino acids have been placed in area 17. Figure 40 illustrates an experiment (Galago 1217L) which can be considered representative of this group. The injection area, depicted in black, is situated a few millimeters behind the 17-18 border. As indicated by the frontal section beneath the cortical reconstruction, the injection went deep into the white matter and even entered the cortex lying within the depths of the calcarine fissure.

In the upper left portion of figure 40, two sections through the superior colliculus have been illustrated; section 51-5 is more caudal. This experiment makes several points. First, area 17 projects exclusively to the upper layers (SZ, SG, and SO) with the density of projection varying with the lamination pattern. In the more rostral tectal section, in the pulv n.

The silver grains

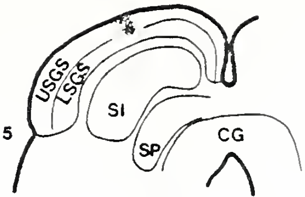
Figure 40. To show the distribution ~~and density~~ of autoradiographic label in the superior colliculus and thalamus after an injection of ^{3}H amino acids into area 17 in Galago 1217L. A frontal section through the injection site is shown below the cortical reconstruction. The following conventions apply to the next 6 line drawings. The locus of the injection is depicted in black on the lateral surface of the cortex. The distribution ~~and density~~ of autoradiographic label is represented by fine dots &

& an effort was made to depict the density of the silver grains by varying the density of the fine dots.

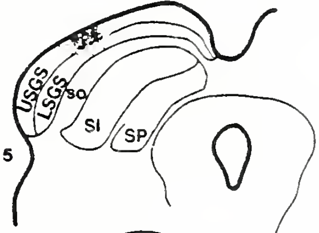
resulting from the transp. of 3H Tritiated amino acid.

from the point of inj., in this case str. cortex

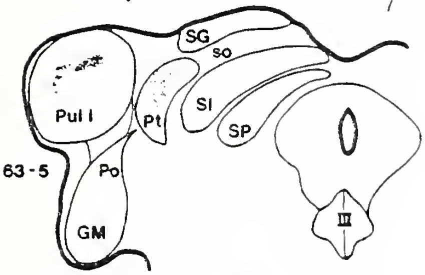
GALAGO
1217 L



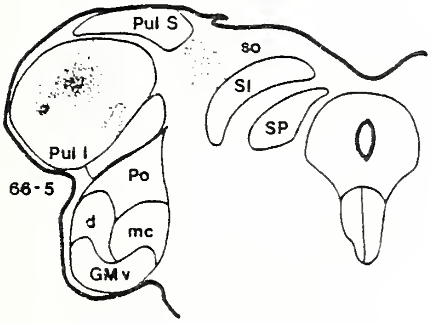
51-5



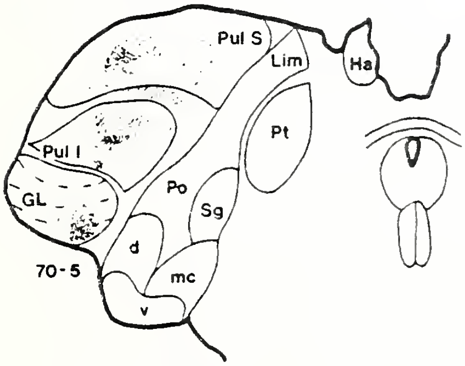
58-5



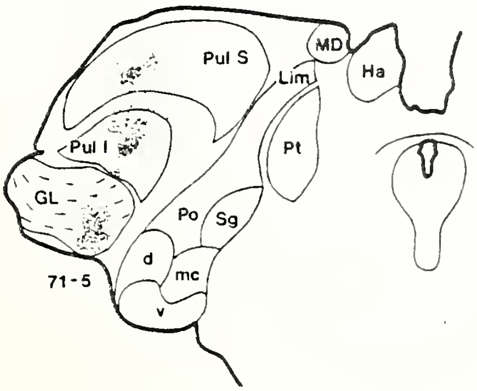
63-5



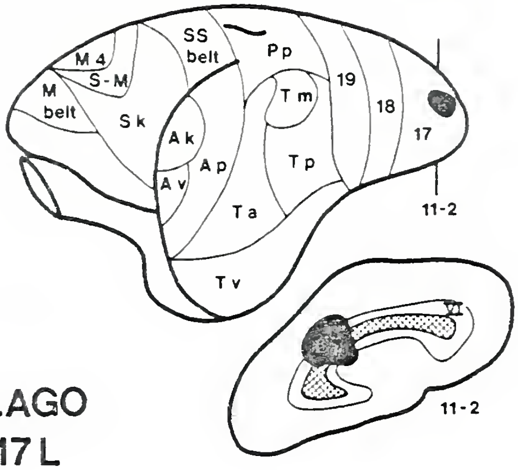
66-5

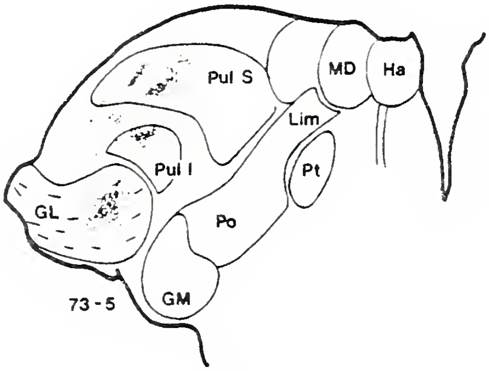


70-5

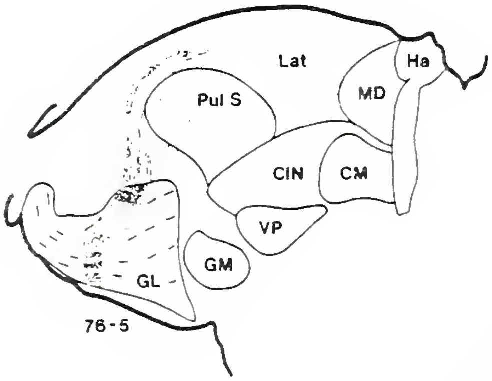


71-5

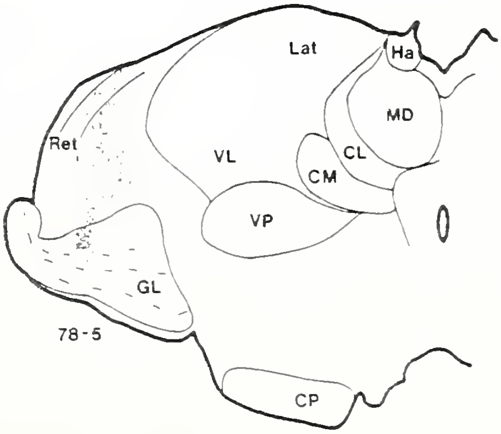




73-5



76-5



78-5

58-5, which lies in the representation of central vision, the distribution of silver grains over stratum zonale and the upper portion of stratum griseum superficiale is uniformly dense, while over the lower portion of the superficial grey lamina the grain density is light. A few grains were observed over stratum opticum as well. No projection to the deeper laminae of the superior colliculus was noted.

As noted above, the injection in this experiment spread into the cortex in the depths of the calcarine fissure. Consequently, a second discontinuous patch of label was observed in the caudal superior colliculus (section 51-5) in the representation of the peripheral visual field. Again, the corticotectal terminals are restricted to the superficial layers; however, the grain distribution over the stratum zonale and the upper half of stratum griseum superficiale is less uniform than that observed in the representation of central vision. Grains are evenly distributed over stratum zonale and the lower portion of the upper half of stratum griseum superficiale. Over the superficial portion of the upper half of stratum griseum superficiale, however, there is a slight decrease in grain density. A sparse projection to the lower half of stratum griseum superficiale was also observed. Few grains were seen below the superficial grey laminae, and these terminations were located in the stratum opticum. The posterior part of the pretectum also contained silver grains after this injection.

Turning to the projections to the thalamus, two columns of label

are observed in the dorsal lateral geniculate body. The more caudal column begins in section 70-5 and passes evenly through all six layers. The position of the label is significant; it is close to but not adjacent to the zero vertical meridian which lies along the mediodorsal border of the dorsal lateral geniculate body. A second column of label, lateral to the first and closer to the monocular segment, appears in section 76-5, and it too continues through all six layers.

Having demonstrated that the entire visual field is represented onto the dorsal lateral geniculate body and the superior colliculus, it is important to determine whether the entire striate cortex projects back onto the pulvinar. Indeed, there are two loci of label in the pulvinar nucleus and this is the main point of this experiment. The first pattern constitutes an arc oriented in the rostrocaudal plane, one arm of which is in the inferior pulvinar and one in the superior pulvinar. These two arms probably merge just rostral to section 73-5. Note that both patches of label are close to, but not adjacent to, the representation of the zero vertical meridian located at the common border between the two pulvinar nuclei. A second pattern of label is observed in sections 66-5 through 71-5 in the inferior pulvinar, extending along the ventral and medial border of the nucleus, and no doubt lies in the representation of peripheral vision.

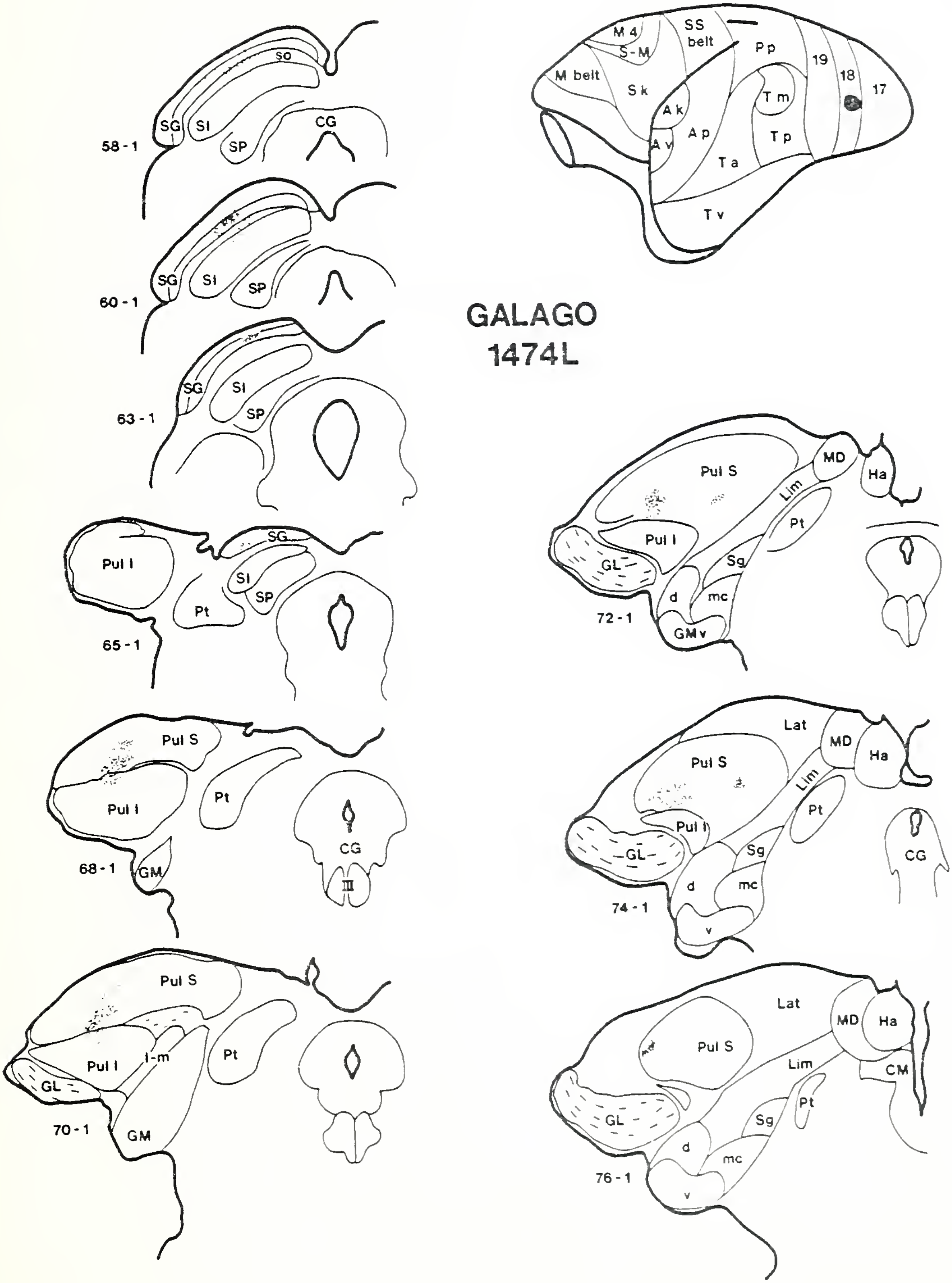
Injection of area 18. Three injections were placed in area 18. Figure 41, illustrating experiment 1474L, summarizes the pattern of the

descending cortical terminations resulting from an injection which abuts but does not extend over the 17-18 border. In contrast to the pattern of projection after an area 17 injection, the heaviest accumulation of silver grains in the superior colliculus was over the lower half of stratum griseum superficiale. Grains were also observed over the deepest part of the upper half of stratum griseum superficiale and the upper extent of stratum opticum. Grain accumulation was sparse over stratum zonale and the superficial portion of the upper half of stratum griseum superficiale. In this experiment no transport to the pretectum was observed.

The label in the pulvinar is centered in the very middle of the complex, on the common border between the inferior and superior divisions. Again, the distribution of silver grains forms an arc with one limb in each subdivision. It is very likely that this distribution of terminals overlies the representation of the zero vertical meridian. No label was observed in the dorsal lateral geniculate body.

Injection of area 19. The pattern of cortical terminations in the tectum and thalamus following an area 19 injection (see *Galago* 1416R, figure 42) is quite distinct from that observed in the previous two experiments. In the superior colliculus, the grain density is heaviest over stratum opticum, moderate over the lower half of stratum griseum superficiale, and sparse over the upper half of stratum griseum superficiale. A few grains were observed over stratum intermediale. In the pretectum, terminal label was observed throughout the entire extent of

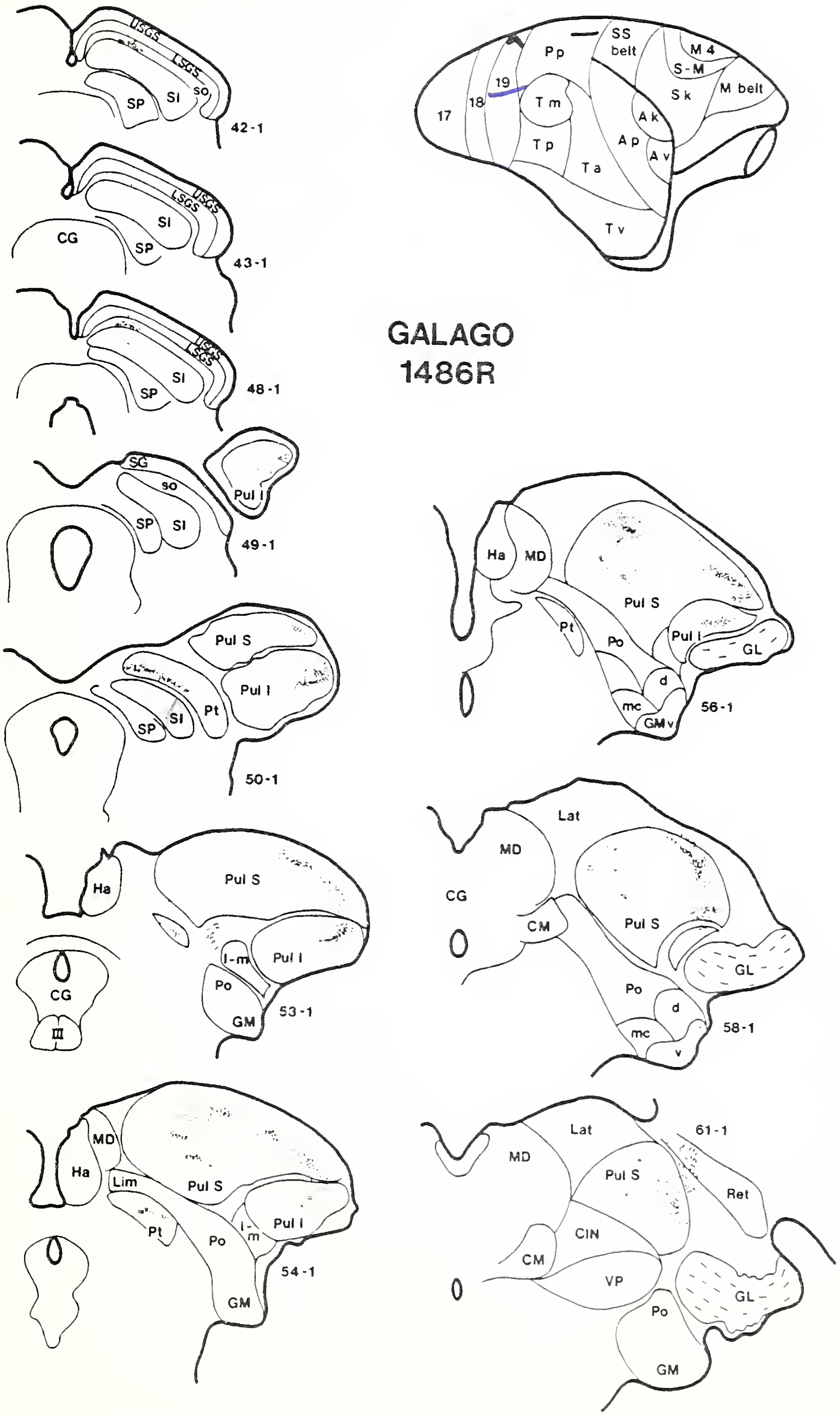
Figure 41. To show the distribution and density of autoradiographic label in the superior colliculus and thalamus after an injection of ^3H amino acids into area 18 in Galago 1474L.



GALAGO
1474L

Figure 42. To show the distribution and density of autoradiographic label in the superior colliculus and thalamus after an injection of ^3H amino acids into area 19 in Galago 1486R.

GALAGO
1486R



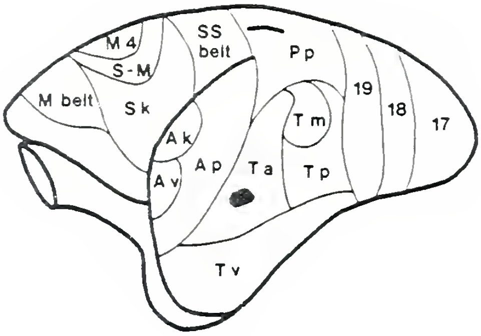
the nucleus.

In examining the distribution of silver grains in the pulvinar complex, several points should be noted. First, while label can be found throughout the entire extent of the complex, most of the projection is concentrated in the superior division. Second, although the distribution of grains appears to be concentrated in two distinct loci, the pattern of label in section 54-1 suggests that the grains form one continuous arc. This arc begins ventrally at the caudal tip of the inferior pulvinar, and crosses over into the lateral portion of the superior division and continues along the lateral margin of the nucleus. This band then sweeps across the dorsal portion of the superior division and curves around and down the medial part of the nucleus, forming nearly a complete circle.

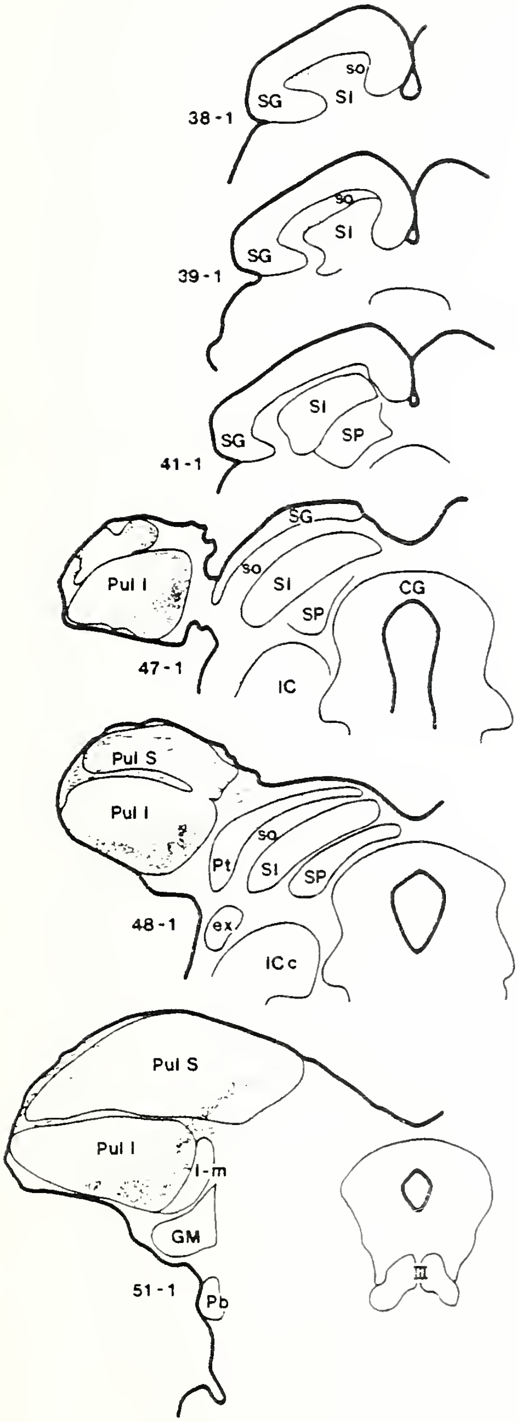
Injection of the anterior temporal area (Ta). Four injections have been made in area Ta and a representative case (Galago 1486L) has been illustrated in figure 43. The projection to the superior colliculus is concentrated in the caudal pole of the structure, confined primarily to stratum opticum. A few grains were observed overlying stratum intermediale. From a comparison of visual field maps of the tectum (Allman et al., '72), this projection is situated in the representation of the periphery. Silver grains were also observed in the posterior pretectum.

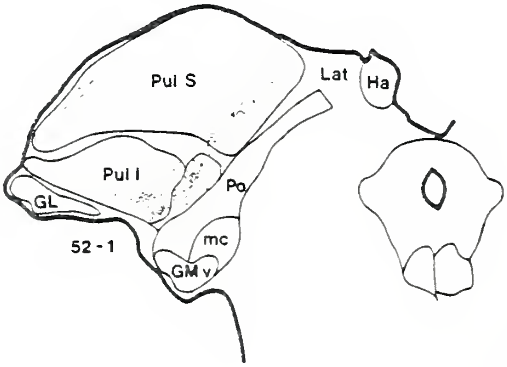
In the pulvinar complex, the focus of autoradiographic label is situated at the ventral border of the caudal inferior pulvinar. As the projection continues rostrally, it turns such that its long axis is now

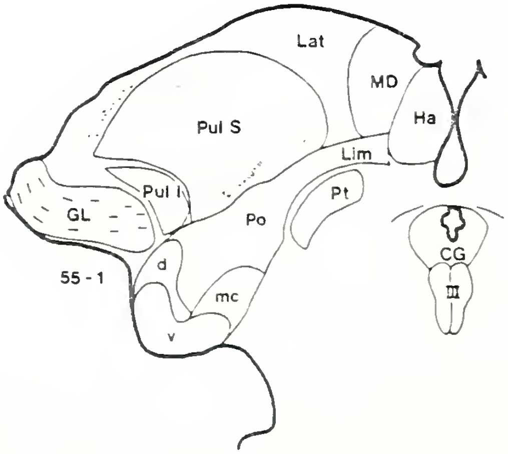
Figure 43. To show the distribution and density of autoradiographic label in the superior colliculus and thalamus after an injection of ^3H amino acids into area Ta in Galago 1486L.



GALAGO
1486L





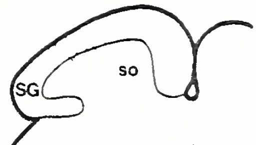


dorso-ventral. At this level (section 51-1) the band of label is adjacent to the medial border of the inferior division and extends over the fiber bundle into the medial portion of the rostral superior pulvinar. At the most rostral level illustrated (section 55-1), a second patch of label is observed along the lateral edge of the superior division in a manner reminiscent of that seen after area 19 injections. If the area 18 injection (Galago 1474L) is used to define the position of the zero vertical meridian, then the projection in this experiment is located in the representation of the peripheral visual field.

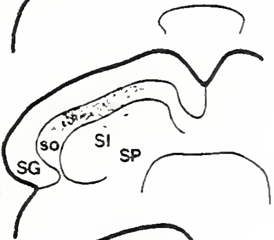
Injection of the middle temporal area (Tm). Figure 44 (Galago 1507L) illustrates an injection of tritiated amino acids focused in the rostral portion of area Tm and extending into the adjacent area Ta. In the superior colliculus, silver grains are present throughout much of the nucleus and concentrated over three laminae. Caudally, a moderate accumulation of grains was seen over stratum griseum superficiale and stratum opticum. Advancing rostrally, the density of grains is greatest over stratum opticum. A few grains were also observed over the superficial part of stratum intermediale. Based on a comparison between this and the previous experiment, it would appear that, with the possible exception of the label in the caudal stratum opticum, the pattern of label in the colliculus can be attributed to the effect of injecting area Tm. The caudal portion of the pretectum was heavily labeled following this injection.

The distribution of label in the pulvinar complex is quite complicated

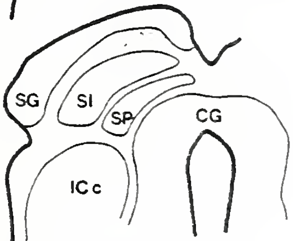
Figure 44. To show the distribution and density of autoradiographic label in the superior colliculus and thalamus after an injection of ^{3}H amino acids into area Tm in *Galago* 1507L.



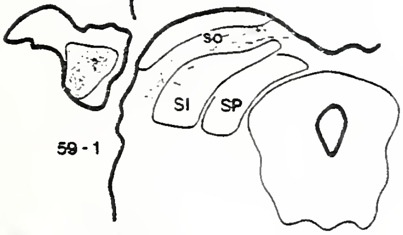
47 - 1



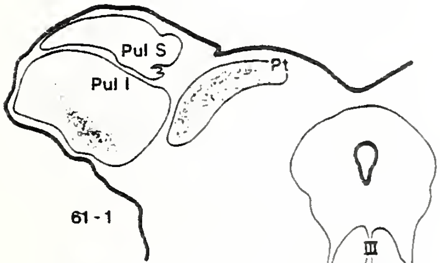
51 - 1



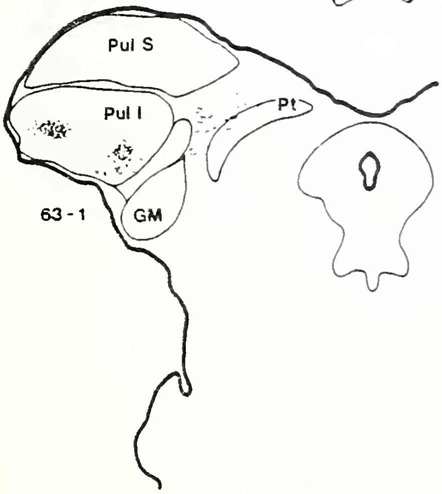
55 - 1



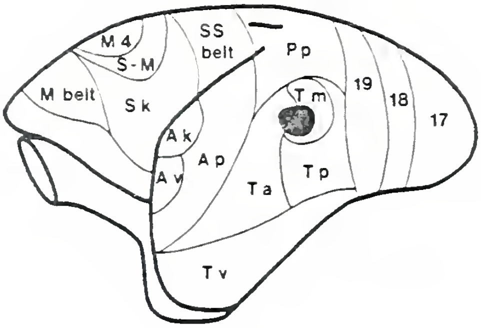
59 - 1



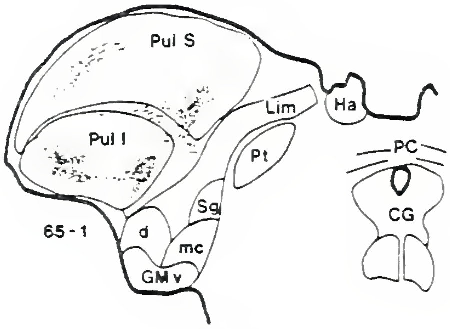
61 - 1



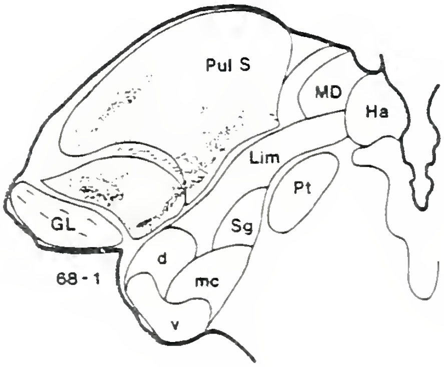
63 - 1



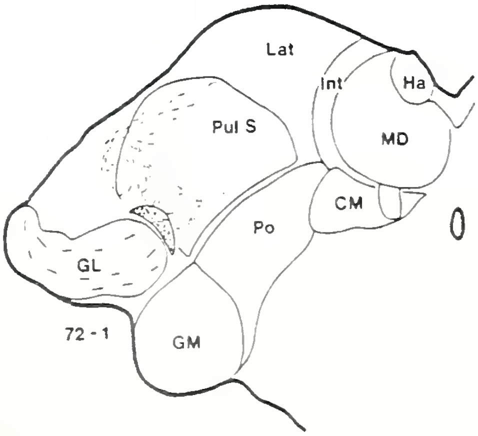
GALAGO
1507L



65 - 1



68 - 1



72 - 1

owing to the fact that the injection involves both areas Tm and Ta. Two foci of label are present. One band is situated ventromedially in the caudal inferior pulvinar, which, when followed rostrally, turns dorsally and extends along the medial border of both subdivisions. At this level (section 68-1), a second patch of label is present along the lateral border of the superior pulvinar. This pattern, of course, is reminiscent of that just described following an injection in area Ta. The main difference between this experiment and the previous one is the presence of label in the lateral portion of the inferior division. This column of label begins at the caudal pole of the inferior pulvinar and continues rostrally, occupying a position along the lateral portion of the nucleus, some distance away from the zero vertical meridian. The band maintains this position throughout the entire extent of the inferior pulvinar nucleus, until at the rostral cap, where it fills the entire structure.

Injection of the posterior temporal area (Tp). Galago 1460R, illustrated in figure 45, summarizes the effect of injecting area Tp. In this experiment no label was observed above background in the superior colliculus or pretectum. Whether this reflects the absence of a projection to the midbrain or a projection beyond the sensitivity of the method cannot be answered. However, it is noteworthy that in the opposite hemisphere of this animal an injection was made in area Ta with the result that silver

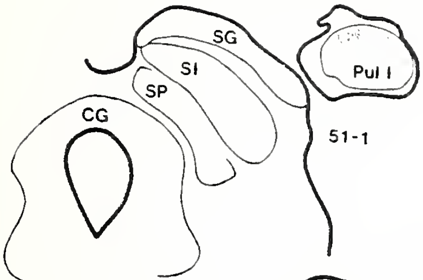
grains above background were observed overlying the superior colliculus.

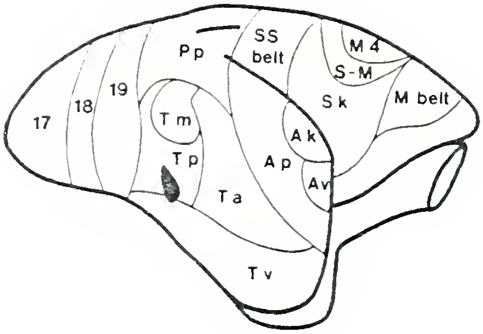
The pattern of label in the pulvinar in this case involves both subdivisions and extends through much of its length. Beginning caudally, a patch of label is centered along the dorsal border of the inferior division. Advancing rostrally, this band shifts slightly medially in the inferior division and crosses over the fiber bundle into the superior division forming a narrow column oriented in the dorsoventral plane, and dividing the subdivision nearly in half. This column maintains this position into the rostral superior pulvinar where it breaks up into small clusters of label.

Injection of the ventral temporal area (Tv). Three injections have been placed in area Tv, one of which (*Galago* 1480R) is illustrated in figure 46. No projection to the midbrain was observed in this experiment, although an injection of area Ta in the opposite hemisphere produced label in the superior colliculus.

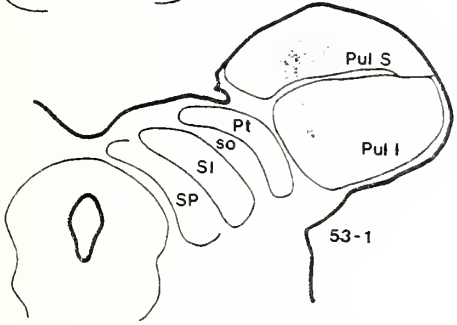
In the thalamus, the greatest concentration of label is found along the medial border of the caudal superior pulvinar. This column of label continues ventrally across the fiber border into the most dorsomedial sector of the inferior division. No label was observed rostrally in the pulvinar complex.

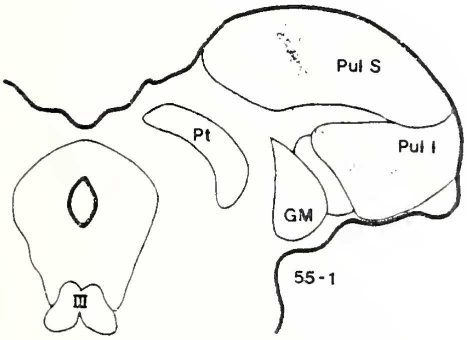
Figure 45. To show the distribution and density of autoradiographic label in the superior colliculus and thalamus after an injection of ^{3}H amino acids into area Tp in Galago 1460R.

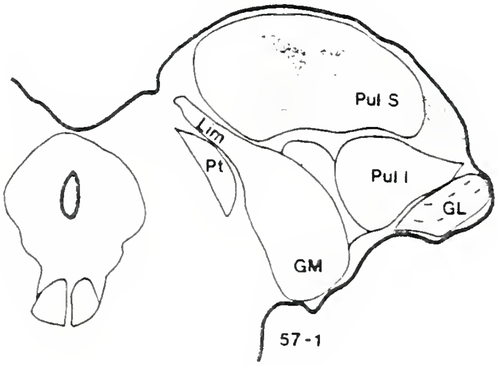


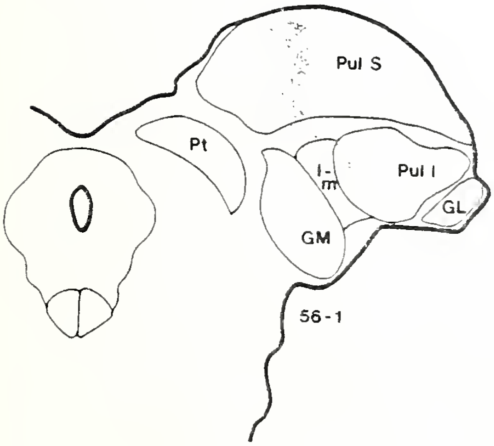


GALAGO
1460R









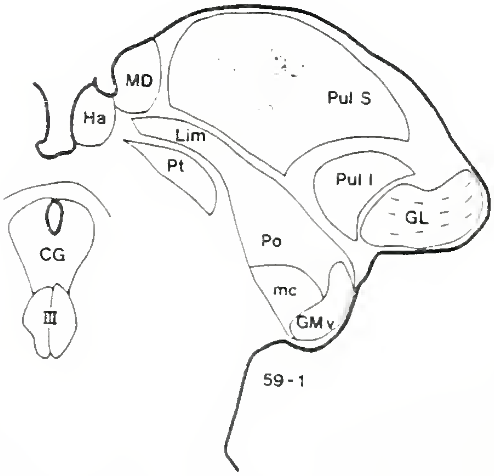
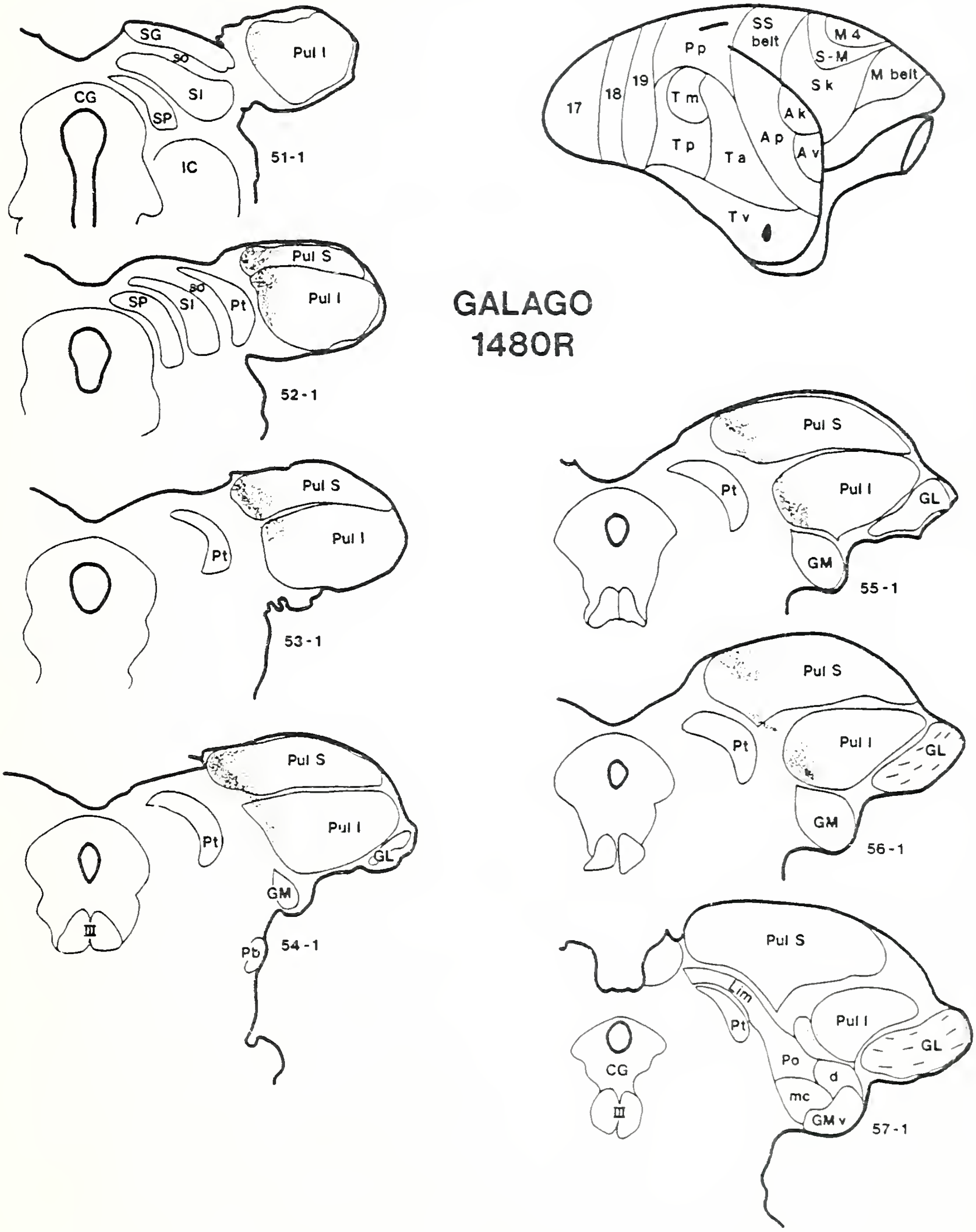


Figure 46. To show the distribution and density of autoradiographic label in the superior colliculus and thalamus after an injection of ^{3}H amino acids into area Tv in *Galago* 1480R.



GALAGO
1480R

DISCUSSION

In the previous four Results sections, the connections of the tecto-pulvinar path in Galago have been examined using different experimental methods and strategies. Indeed, the rationale for organizing the Results into sections was based on differences in experimental techniques. However, these individual sections are united in one very important way: Each experimental strategy demonstrates the functional unity of the pulvinar nucleus and the cortex with which it is connected. For example, section two makes the point that the entire pulvinar is the recipient of fibers from the superficial layers of the superior colliculus. Section one shows that the pulvinar projects to the entire occipital and temporal lobes (excepting the auditory field). Sections two, three, and four show that the entire tecto-pulvinar path is the recipient of descending fibers from the occipital and temporal lobes.

Since each section makes its own special contribution to understanding the organization of the tectopulvinar path, the significance of these results initially will be discussed separately. Then, general issues which unite all four studies will be discussed.

Injections of HRP into the Visual Cortex

The results show first that the pulvinar nucleus projects to an extensive area of cortex that includes all of the occipital lobe, most of the temporal lobe (only the auditory areas are excluded), and very likely portions of the posterior parietal area as well. To emphasize just how extensive this field is, we estimate that it may comprise as much as one-half of the entire neocortex. The significance of this finding is that the projection field of the pulvinar nucleus can be equated to visual cortex.

The visual nature of the pulvinar nucleus in primates and many other species is well documented. Fibers from the superficial layers of the superior colliculus are distributed to the entire pulvinar nucleus in the tree shrew (Harting et al., '72a). In primates, the superior colliculus also projects to the pulvinar complex, but only to a limited portion of the nucleus. In Galago, Glendenning et al. ('75) described the superior colliculus as projecting to only the caudal half of the inferior pulvinar nucleus. Similar findings have been reported in new world (Mathers, '71) and old world (Benevento and Fallon, '75) monkeys. Partlow et al. ('77) recently extended the tectopulvinar projection to include the entire inferior pulvinar nucleus in the rhesus monkey. Experimental studies of the descending subcortical projections of the striate cortex in primates demonstrate that portions of the pulvinar complex are also the recipients of a substantial visual cortex input. In

Galago, Symonds and Kaas ('78) conclude that a central "core" of the pulvinar complex receives a projection from area 17, while in the rhesus monkey the lateral and inferior subdivisions receive projections from the striate cortex (Campos-Ortega and Hayhow, '72; Ogren and Hendrickson, '76). However, it was not until HRP was injected into the pulvinar nucleus of *Galago* (see Results, II) that the full extent of the visual input to the pulvinar nucleus emerged. *All* parts of the pulvinar nucleus receive projections from the superficial layers of the superior colliculus *and* from the striate cortex. Thus the pulvinar nucleus turns out to be a visual relay nucleus, and the cortex to which it projects can be regarded as primary visual cortex as that term has been used since the days of Flechsig (see Diamond, '78).

The vast visual field can be subdivided and an important question arises. Do the architectonic subdivisions have functional significance? To answer this question, it is important to define a functional unit. In an earlier study of the cat auditory cortex (Winer et al., '77), we concluded that architectonic subdivisions were functionally significant. First, this area had been defined on the basis of cytoarchitecture (Rose, '49) and sensory electrophysiology (Woolsey and Walzl, '42; Rose and Woolsey, '49). Our results supported the cortical parcellation by demonstrating that each cortical subdivision has unique connections. Furthermore, we argued that the thalamic subdivisions, as defined by differences in their projections to the cortex, were the targets of

different ascending tracts.

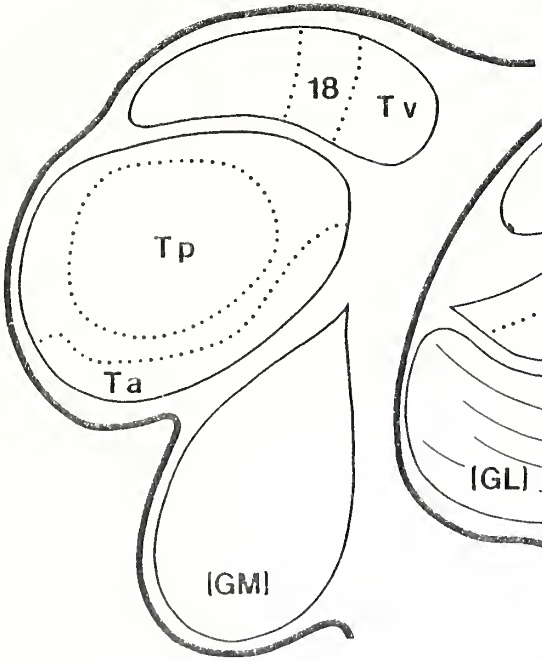
On the basis of these criteria, there is one significant way to divide the whole visual field of *Galago* and that is to distinguish between the striate cortex and the rest of the pulvinar target. There is hardly any need to defend the concept that the striate cortex is a functional unit. Area 17 has been defined by morphological criteria (Glendenning et al., '76; Diamond, '78) and by electrophysiological mapping studies (Woolsey, '71), and we have demonstrated that only area 17 receives overlapping projections from both the dorsal lateral geniculate body and the pulvinar complex.

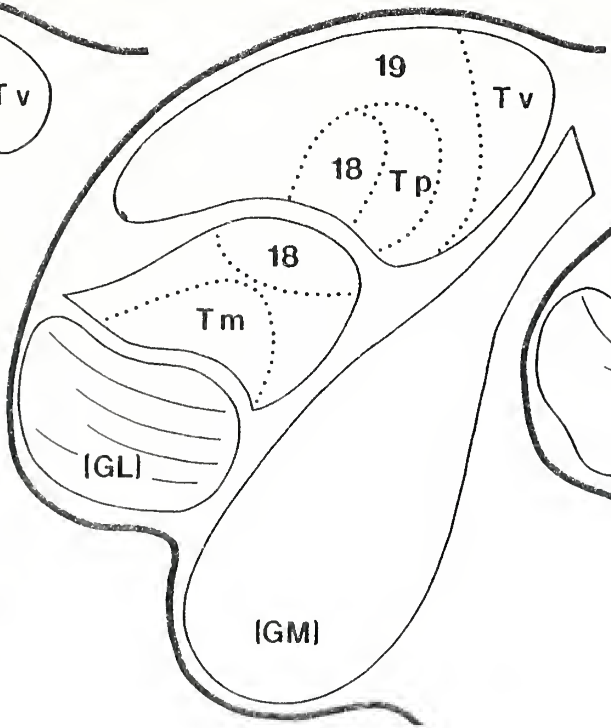
The question then remains to what extent are the subdivisions of the extrastriate cortex functionally significant? Although we have identified several subdivisions of the posterior neocortex on the basis of cytoarchitectonic features, and have demonstrated that each subdivision is uniquely connected with the pulvinar complex, by themselves these findings are *not* sufficient to conclude that each cortical subdivision is functionally different. A case might be made for separate units if the distributions of labeled cells were identical for two remote cortical points in the same area and strikingly different for two neighboring points on either side of a border. Evidence has been presented which supports the conclusion. Thus, injections of HRP into area 18 *always* label cells on either side of the common border formed by the two architectonic subdivisions of the pulvinar nucleus. On the other hand, injections of

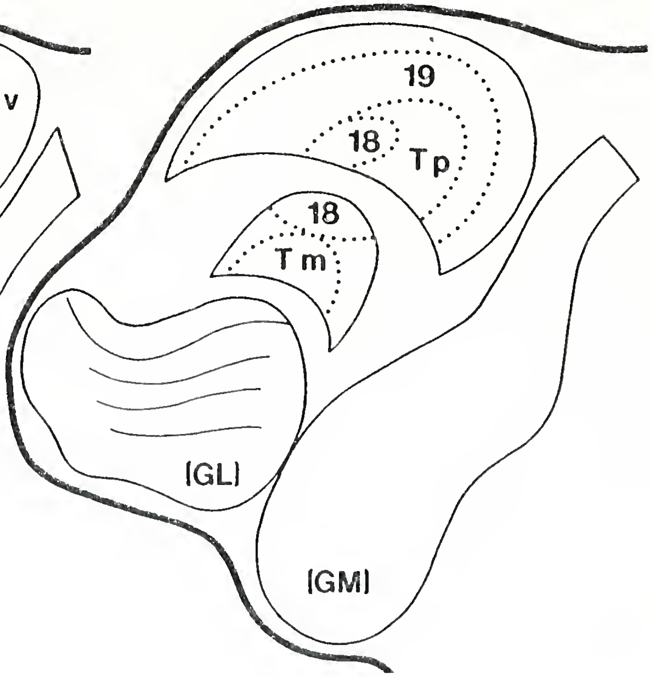
HRP into the adjacent area 19 result in labeled cells concentrated in the superior division forming an arc sweeping across the dorsal border of the nucleus. Thus, injections in adjacent cortical areas do not necessarily label cells in adjacent portions of the pulvinar complex.

As it stands, an alternative explanation is that the entire temporal lobe constitutes one representation of the retina and the spatial organization of the projections of the pulvinar reflect the fact that the retina is represented once topographically in the inferior pulvinar and again in the superior pulvinar. However, there are several findings which argue against the idea that there is one simple topographic projection of the entire pulvinar to the entire extrastriate cortex. First, there is considerable overlap in the cortical projections of the pulvinar complex which can be overlooked when we try to identify the focus of the concentration of labeled cells. For example, labeled cells are located in the caudal extremity of the inferior division after almost every injection. Second, if there were a simple spatial order then it would follow that injections in adjacent cortical areas would label cells in adjacent regions of the pulvinar nucleus and that is not necessarily so (see previous paragraph and Fig. 47). Finally, injections into the different cortical subdivisions do not produce the same "patterns" of labeled cells in the pulvinar nucleus. Of course, the same pattern can occupy a different position within a nucleus. Thus, in the case of area 17 injections, labeled cells always form a column through all six layers of the lateral

Figure 47. A schematic drawing of three levels of the pulvinar complex showing the locus of greatest concentration of labeled cells resulting from an injection in each subdivision of the visual cortex, excepting area 17. This diagram does not attempt to show regions of the pulvinar where conspicuous overlap occurs. For example, almost every injection labeled some neurons in the caudal sector of the inferior pulvinar nucleus. Certainly, there is overlap in the patterns of labeled cells following injections into areas 18 and Tm. Nonetheless, from any given distribution of labeled cells, one can predict with considerable confidence the cortical site of injection.


18
Tv
Tp
Ta
[GM]


19
Tv
18
Tp
18
Tm
[GL]
[GM]


19
18
Tp
18
Tm
[GL]
[GM]

geniculate body, and the column varies in position with respect to the locus of the cortical injection. But, while the labeled cells following HRP injections in the different regions of the extrastriate cortex occupy different loci within the pulvinar nucleus, no common distribution of labeled cells is revealed. After some injections, the band of labeled cells is very long and narrow; in others the whole section through the caudal inferior pulvinar is filled with labeled cells. In some experiments, the focus of concentration is in the inferior division, while in others it is located in the superior division.

So we must leave this question to rest with only tentative conclusions. Certainly, on the basis of architectonics (Allman et al., '73; Diamond, '78), electrophysiological mapping studies (Allman et al., '73) and differences in patterns of projections with the pulvinar nucleus, areas 18 and Tm can be considered functional units. At the same time, it seems possible that the differences between areas Ta and Tp simply reflect the fact that different parts of pulvinar represent different parts of the visual field. However, these regions of the extrastriate cortex could also be considered functional units inasmuch as each is the recipient of a unique pattern of connections from the pulvinar representing different portions of the visual field and, as such, may represent some unique contribution to the physiological state of perception.

The main conclusions of this study support and refine the conclusions reached by the methods of tracing retrograde and anterograde

degeneration. To summarize the retrograde evidence briefly, ablation of areas 17 and 18 leads to retrograde changes in the dorsal lateral geniculate body and on either side of the common border formed by the two subdivisions of the pulvinar nucleus. If this ablation is enlarged to include the dorsal portion of area 19, then the lateral edge of the superior pulvinar nucleus degenerates (see figure 6, Atencio et al., '75). Ablation of the middle temporal cortex (Tm) alone produces slight to moderately severe degeneration in the inferior pulvinar (Wilson and Diamond, experiments in progress). Small lesions of the cortex ventral to area Tm fail to produce any thalamic retrograde degeneration. When the lesion is enlarged to include considerable portions of the cortex below Tm, a pattern of retrograde changes appeared in the pulvinar complex which was inexplicable at the time. Moderate to heavy degeneration was present in the ventromedial portion of the inferior pulvinar (Tr) and in two separate loci in the caudal superior pulvinar nucleus. Degeneration was also present in the dorsal lateral geniculate nucleus which was assumed to result from interruption of geniculate radiations to area 19 (Atencio et al., '75). We can now specify that the degeneration in Tr represents a result of involvement of cortical area Ta, while the presence of degeneration in the medial sector of the superior pulvinar is reminiscent of the pattern of label following HRP injections into area Tv. Finally, the degeneration in the lateral portion of the superior pulvinar is probably due to undercutting visual radiations.

Our experiments show why small lesions in the extrastriate cortex fail to produce retrograde changes in the thalamus (Atencio et al., '75; Wilson and Diamond, experiments in progress). We now know that the pulvinar projects topographically onto both area 17 and the extrastriate cortex. Thus, small lesions in the temporal lobe may not produce retrograde changes since the transected neurons are "sustained" by collateral projecting to area 17.

Turning now to studies of anterograde degeneration, once again the present results support and refine the earlier conclusions. For example, lesions of the caudal part of the inferior pulvinar (see figure 32, Glendenning et al., '75) produced two foci of cortical degeneration, one in area Tm and another in the cortex below Tm. We support this conclusion by showing that the best way to label neurons in the inferior pulvinar is to inject areas Tm and Ta. We can also refine our picture of the cortical projections of the pulvinar nucleus since we have shown that the pulvinar projects to area 17 (Raczkowski and Diamond, '78a). Furthermore, we would argue now that both subdivisions of the pulvinar complex project to each subdivision of the visual field.

In view of the evidence presented which suggests that the pulvinar nucleus is visual in function, it is important to determine whether portions of the complex are visuotopically organized. Previously, Allman et al. ('72), using electrophysiological mapping techniques, have presented evidence for a topographic representation of the visual field in

the inferior pulvinar nucleus of the owl monkey. The representation of the central 10° of the visual field are located dorsally and rostrally, while more peripheral parts of the visual field are located more ventrally. The extreme periphery is represented along the ventral border of the inferior pulvinar, adjacent to the medial geniculate body. Our injections into the striate cortex and the pulvinar complex support these findings. First, when the injection is on the lateral surface of the striate area, not far from the border with area 18, labeled cells are distributed along the dorsal aspect of the inferior division. Second, if the injection is located in the representation of the peripheral field on the medial wall of the striate cortex, the labeled cells are found in a sheet along the ventral border of the inferior division. Third, when injections of HRP are placed in the lateral portion of the inferior subdivision, labeled cells are concentrated in the medial portion of the superior colliculus in the representation of the upper visual field (Lane et al., '73). Finally, medially placed injections in the inferior division label cells in the lateral portion of the superior colliculus where the representation of the lower visual field is located. These findings are consistent with the conclusions derived from lesion studies in the rhesus monkey by Campos-Ortega and Hayhow ('72) and Partlow et al. ('77).

Our results also suggest that the superior pulvinar contains a topographic representation of the visual field which is a mirror image of that described for the inferior pulvinar. Thus, central vision is

represented ventrally in the superior division and more peripheral parts of the visual field are represented dorsally. The upper visual field is located laterally and the lower visual field is represented medially.

In this final section we will examine if there are features of the tectopulvinar path of Galago which are shared by other mammalian species. With regard to the organization of the pulvinar interconnections with the cortex, several issues need to be mentioned. First, recent studies in both cat and monkey have reported the presence of bands of labeled cells in the dorsal thalamus following injections of HRP into the cortex (Berson and Graybiel, '78; Kievet and Kuypers, '77; Wong-Riley, '77). Furthermore, these intricate arrangements of slab-like zones appear to hold for corticothalamic connections as well (Benevento and Davis, '77; Wong-Riley, '77). Second, regarding the issue of overlap, it has been shown in both cat and in monkey that at least some of the thalamic subdivisions in the posterior thalamus may project to more than one cortical field. For example, in monkey both the inferior and lateral subdivisions of the pulvinar complex project onto areas 18 and 17 and this connection is reciprocal (Benevento and Rezak, '76; Wong-Riley, '77). Third, comparing specific connections in Galago with reports in other primates, our finding that the pulvinar nucleus projects to area 17 confirms the previous finding of Ogren and Hendrickson ('76, '77) and Benevento and Rezak ('75) using the autoradiographic method.

It has been shown by Wong-Riley ('77) and Benevento and Davis ('77)

that area 18 is especially connected with the common border formed between the inferior and lateral subdivisions of the pulvinar nucleus. Finally, Lin et al. ('74) have demonstrated, using the HRP method, that the tecto-recipient zone of the inferior pulvinar in the owl monkey projects to area Tm, confirming a similar projection in Galago.

HRP Injections into the Pulvinar Nucleus

This series of experiments makes three chief points. The results show first that the entire pulvinar nucleus receives fibers from the superficial layers of the superior colliculus and, second, that it is the cells in the lower half of stratum griseum superficiale which give rise to this projection. The third point concerns the topographic and laminar precise origin of neurons giving rise to the descending cortical projections to the pulvinar nucleus.

Turning to the first main conclusion, it had been shown by Glendenning et al. ('75) that the superficial layers of the superior colliculus project topographically onto the caudal inferior pulvinar nucleus. The method of retrograde transport of HRP provides an opportunity to refine this concept of the organization of the superior colliculus inasmuch as the very cells from which the tecto-pulvinar path originates can be identified.

One important finding which was obvious from the first experiment in which HRP was injected into the inferior pulvinar nucleus was that labeled neurons were observed only in the lower half of stratum griseum

superficiale, while the upper half of stratum griseum superficiale was free of labeled cells. The dark grannules resulting from the HRP reaction product often filled the cell soma and outlined considerable portions of the dendritic tree. It was possible therefore to characterize the labeled cells and to thereby distinguish the form of the cells projecting to the pulvinar nucleus. This effort to identify and classify the cell types was inspired by a Golgi study of the superior colliculus by Langer and Lund ('74). These authors distinguished several types of neurons in the superficial grey, one of which is located just above the opticum layer. This class of neuron, termed "wide field vertical cell" is characterized by an ovoid soma with the long axis parallel to the tectal surface and with dendritic trunks emerging from the opposite poles of the soma's long axis. This describes exactly the cells labeled with HRP after injections into the pulvinar nucleus (see Raczkowski and Diamond, '78b).

Most important for our long-range purposes is the discovery that the entire pulvinar nucleus is the target of the superior colliculus. In one experiment, HRP was injected rostrally into the inferior pulvinar nucleus with the result that a few labeled cells were observed in the lower half of the superficial grey lamina. Initially, we thought that this injection had invaded the tecto-recipient zone as defined by anterograde degeneration studies. However, a similar finding occurred when injections were confined to the superior pulvinar nucleus. For example,

in one experiment a small amount of HRP was injected into the caudal superior pulvinar, resulting in labeled cells located in the medial sector of the lower superficial grey lamina. Additional injections placed in other portions of the superior division confirmed this finding.

While a projection from the superior colliculus to the pulvinar complex is certainly part of the mammalian plan (Harting et al. '72; Diamond and Hall, '69), the question as to whether there are species differences is now an open question. Previously, a great importance was attached to the difference between the tree shrew and Galago with regard to the extent to which the pulvinar is innervated by tectal fibers (Harting et al., '72a; Glendenning et al., '75). In the tree shrew, the entire pulvinar nucleus is the target of the superficial layers of the superior colliculus, while in Galago it was thought that large sectors of the pulvinar nucleus were devoid of tectal input. We now know that this is no longer the case; the entire pulvinar nucleus of Galago receives fibers from the superficial layers of the superior colliculus. In the same light, one wonders about the tectal projections to the pulvinar complex in squirrel (Robson and Hall, '77), cat (Graybiel, '72), and other primates (see Partlow et al., '77).

We are aware of only two other reports in which the projections from the superior colliculus to the pulvinar have been examined with the HRP method, one in tree shrew (Albano et al., '77) and the other in rhesus monkey (Trojanowski and Jacobson, '75). The latter study makes

the point that the superior colliculus contained labeled cells after injections placed in the inferior and lateral subdivisions of the pulvinar complex. This result stands in contrast to other reports using anterograde methods in which only the inferior pulvinar was shown to project to the superficial layers of the superior colliculus (Benevento and Fallon, '75).

The third chief finding regards the cells of origin of cortical descending pathways to the pulvinar complex. At the outset we expected to find that layer V projects to the tectum and layer VI projects to the thalamus (Gilbert and Kelly, '75; Lund et al., '75). Our own injections into the dorsal lateral geniculate body and the superior colliculus confirmed these findings (Raczkowski and Diamond, '78). However, when we injected HRP into the pulvinar nucleus, we not only observed labeled cells in layer VI in the extrastriate cortex, but also observed labeled cells in layer V of area 17. Since layer V of area 17 had been shown to project to the tectum, the question arose as to whether the HRP entered axons passing through the pulvinar en route to the tectum. To answer this question, tritiated amino acids were injected into area 17 with the result that patches of silver grains representing terminal endings were observed in both subdivisions of the pulvinar complex (see Results, IV, and Symonds and Kaas, '78). From a survey of all injections placed into the pulvinar, we conclude that the pulvinar nucleus receives projections from both layer VI neurons and layer V pyramidal cells, and that the

layer V neurons are located in area 17, confirming earlier reports by Lund et al. ('75) and Trojanowski and Jacobson ('77) in the rhesus monkey, There is one notable exception. Injections in the superior pulvinar, away from the common border with the inferior subdivision, label cells in layer V as well as layer VI, but the layer V neurons are not located in area 17. The significance of this puzzling difference remains obscure.

Considering the topography of the descending projections to the pulvinar nucleus, injections located in the caudal inferior pulvinar nucleus label a sheet of layer VI neurons extending across areas Tm and Ta. When the injection is more rostrally placed in the nucleus, the sheet of layer VI labeled cells shifts into areas 19 and 18. A similar organization is observed following injections into the superior subdivision. The projections from area 17 onto the pulvinar are also topographic. Laterally placed injections in the inferior pulvinar label cells along the ventral bank of the calcarine fissure, while medially placed injections label cells on the lateral surface. Again, a similar organization is evident in the projection onto the superior pulvinar.

From these experiments we conclude that the entire pulvinar complex is a visual relay nucleus. Neurons originating in the lower superficial grey lamina of the superior colliculus project topographically onto the entire pulvinar nucleus. Second, layer V of area 17 projects onto the pulvinar. Taken together, both findings support the conclusion that

the pulvinar nucleus is especially related to visual functions.

Injections of HRP into the Superior Colliculus

The results show first that nearly all of the neocortex projects to the superior colliculus and, second, that these projections arise exclusively from layer V. Third, the distribution of labeled cells in the cortex is organized in patterns which correspond to architectonic and functional subdivisions. There is no better way to illustrate this point than to cite cases in which a single field is labeled in its entirety by a single injection with few or no cells outside the field.

One such case is experiment 1321L in which the HRP diffused over the superficial grey and optic layers. Although the injection is large, with one exception only the visual cortex contained labeled cells and no visual area seemed to be spared. (There is one notable exception in that the motor belt of the somatic field contains labeled cells, and this anomaly will be explained below.) This finding is not related to just the visual field. In experiment 1571R, an injection was placed in stratum profundum with the result that virtually every neuron labeled was located in the somatic field.

Turning now to a discussion of how these descending projections from the cortex reflect the functional organization of the superior colliculus, our starting point is experiments in which the HRP is confined to individual laminae.

In one case, experiment 1310L, HRP was restricted to the

superficial layers of the tectum. With one exception, all of the labeled cells were located in the visual cortex, in particular, areas 17 and 18. In every case when areas 17 and 18 contained labeled cells, HRP was found in the superficial grey layer above stratum opticum. We conclude that areas 17 and 18 project to the superficial grey layers, probably not to stratum opticum and certainly not to the deeper layers.

In the case where HRP was restricted to the superficial grey lamina, labeled cells were also observed outside the visual field in what we have defined as the motor belt, a subdivision of the somatic field just anterior to motor cortex. In the monkey, a similarly situated area of frontal cortex, area 8, when stimulated produces eye movements, and has been defined as the frontal eye fields. Projections from area 8 to the superior colliculus have been described using degeneration methods (Astruc, '71), and, more recently, anterograde transport methods (Kunzle and Akert, '77; Kunzle et al., '76). Using the autoradiographic method, two patterns of grains were observed overlying the superior colliculus. The first concentration of grains is over stratum opticum and stratum intermediale. A second, narrow band of label is located over stratum zonale. Thus on the basis of connections, it may be concluded that portions of the motor belt cortex in Galago may be homologous with the frontal eye field cortex in higher primates.

The second main point of these injections regards topography of connections. When the pattern of label in the visual field and the site of

injection within the superficial layers is compared with published mapping experiments (Lane et al., '73), the connections appear to be retinotopically organized. For example, the rostral superficial layers where the representation of the vertical meridian is located appear to be especially connected with the 17-18 border. When the injection site is very caudal in the superficial grey, the label in area 17 shifts to the caudal pole.

From a survey of all the present tectal injections, the best way to label neurons in the extrastriate belt is to inject HRP into stratum opticum. While we have no injection confined to this layer, injections involving both the superficial grey and the optic layer produce labeled cells in the entire visual field, lending further support to the notion that the visual field is one functional unit.

Turning to injections in the deeper layers, several points should be noted. First, in contrast to the upper layers, which are exclusively visual, the deeper laminae are recipients of auditory, somatic, and visual inputs. These experiments also demonstrate that not only is there a functional organization within the tectum based on architectonic subdivisions, but also a functional organization depending on differences in the rostrocaudal dimension of the superior colliculus. Whenever an injection is placed in the anterior two-thirds of the intermediate layers, labeled cells are located in the visual and somatic fields. The amount of label in both fields varies with the location of the injection. Thus,

injections superficial and rostral in the intermediate layers result in a majority of labeled cells in the visual field. When the injection site shifts deeper in the intermediate layers the label in the somatic field increases in number.

There are two ways to account for this distribution of labeled cells. Either the two cortical fields converge in the intermediate grey layers or each injection involves at least two separate targets, one being the target of the somatic belt and the other the target of the visual belt. The solution to this issue awaits autoradiographic analysis (see below).

With regard to the auditory field, any injection situated posteriorly in the intermediate layers labeled cells in the auditory field to the virtual exclusion of the other two fields. The auditory subdivisions which contain the majority of label, areas Av and Ap, are connected with the caudal and dorsal divisions of the medial geniculate body, respectively.

To summarize, these results show that all three sensory fields project to the superior colliculus and that each field has a distinct target in the sense that some part of the colliculus may receive projections from one field. Thus, the visual field is best labeled by injections in the upper layers of the superior colliculus. The auditory field is labeled predominantly when the injection is located caudally in the intermediate grey, while the somatic field is populated with labeled neurons when the injection is laterally placed in the deeper layers. This is not to say that

convergence in the tectum does not take place. For example, it is not unreasonable to hypothesize that axon terminals from each of the sensory fields contact the dendrites of single neurons whose cell bodies are located in the deeper layers.

Tritiated Amino Acid Injections into Visual Cortex

The results show first the patterns of descending projections to the pulvinar and the superior colliculus from small areas of the cortex. These findings support the conclusion of previous sections that the visual field is one functional unit united by its common projections to the pulvinar complex. Injections in each of the several subdivisions of the visual field reveal certain distinct patterns of termination in the pulvinar, which are reminiscent of those observed when HRP was injected into the visual cortex. Taken together, these several patterns cover the entire pulvinar nucleus. Indeed, if we construct a schematic diagram of the pulvinar nucleus with the individual patterns of termination following amino acid injections into each cortical subdivision, the picture would be identical to that seen in figure 47. Thus, for example, area 18 projects principally to the common border formed by the two subdivisions of the pulvinar complex, while area Tv sends axons to the most medial sector of the caudal superior pulvinar nucleus.

Again, the results show that the major subdivision of the visual field is between the striate and extrastriate cortex. Thus, area 17

injections project fibers onto the dorsal lateral geniculate body and the pulvinar nucleus, while the extrastriate cortex projects only to the pulvinar complex. In addition, these experiments support the notion that the entire striate cortex projects back onto the pulvinar; recall the injection of area 17 *Galago* 1217L in which the injection spread onto the lateral and medial surface of the striate cortex. Two discontinuous patches of label were observed in the inferior pulvinar, one near the representation of the vertical meridian and the other at the ventral border of the nucleus.

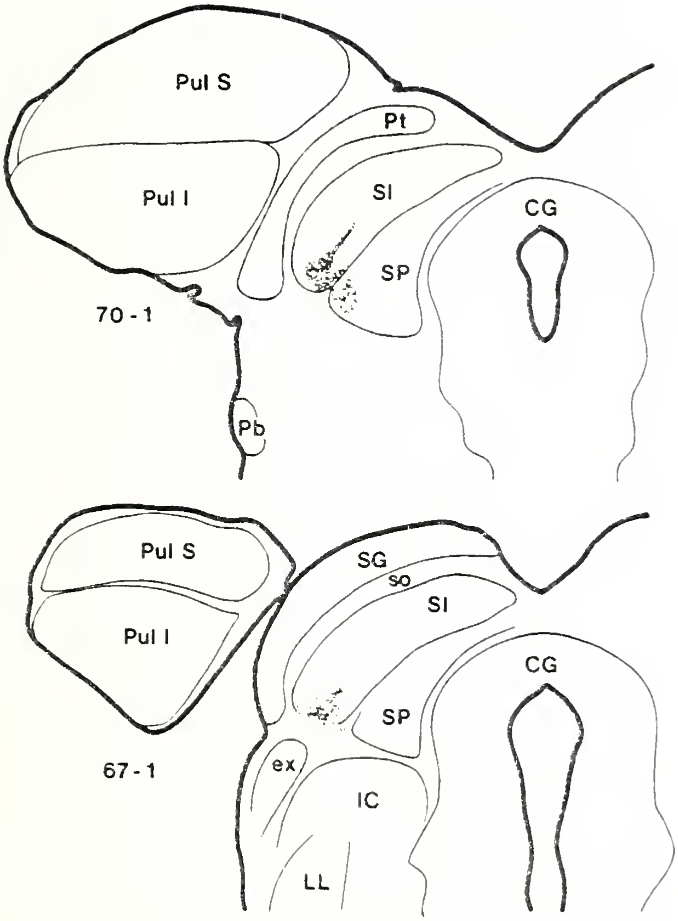
Turning to the patterns of projection to the superior colliculus, in Results section III are described HRP injections in the tectum and these experiments showed that areas 17 and 18 project primarily to the superficial grey and that when the injection spread into stratum opticum labeled cells were contained throughout the visual field. Whether or not any further segregation of inputs occurs was beyond the HRP method. The anterograde experiments described in Results section IV support and refine the view of the functional organization of the tectum described in Results section III. Only injections involving the visual field produce grains overlying the upper layers. In addition, these experiments provide supplemental information regarding how each subdivision of the visual field is connected with the superficial layers. For example, areas 17 and 18 do not overlap extensively in the upper layers. Following an area 17 injection, grains are uniformly distributed primarily over

stratum zonale and the upper half of stratum griseum superficiale. Sparse grains were observed overlying the lower half of stratum griseum superficiale. After injections confined to area 18, the heaviest accumulation of grains is over the lower portion of the superficial grey lamina. Moderate grain densities overlie the upper stratum griseum superficiale.

Second, these experiments support the notion that the deeper layers are the recipients of multimodal input and provide additional information regarding the convergence of projections from the several sensory fields. As the results in Results section IV indicate, the extrastriate visual cortex (excluding area 18) projects to the superficial portion of the intermediate grey and the projection is more prominent rostrally in the tectum. The left half of figure 48 shows the cortical terminations in the deep layers of the superior colliculus following an injection placed in the somatic field. Note that the autoradiographic label is located ventrally in the intermediate layers. Thus it would appear that while both the visual and somatic fields project onto the intermediate layers each sensory field has its own target. Finally, we have examined the descending projections from the auditory cortex and only injections in areas Av and Ap produce label in the deep superior colliculus and it is confined to the caudal aspect of the intermediate grey; this result is shown in the right half of figure 48 (see Fitzpatrick et al., '78). No projections were traced rostrally in the superior colliculus

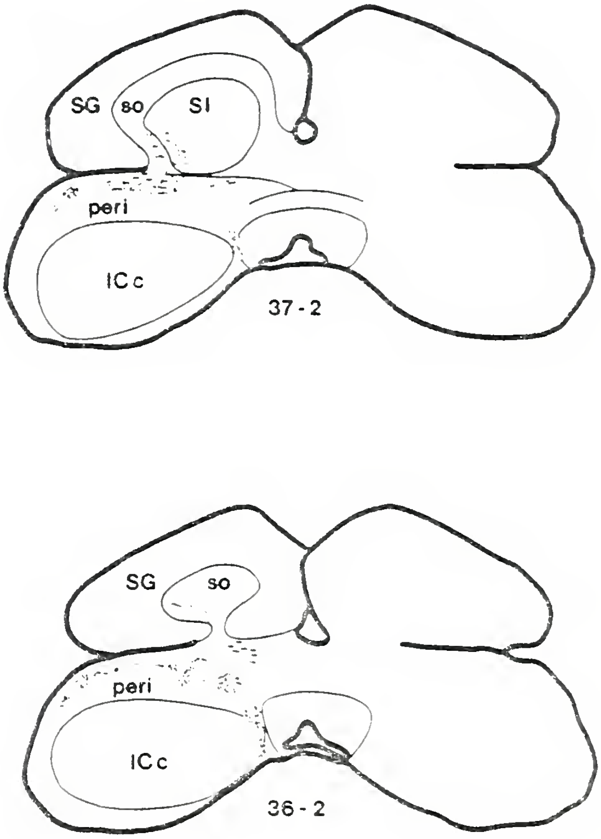
Figure 48. To show the distribution and density of autoradiographic label in the superior colliculus after an injection into the somatic cortex (left side of figure) and into the auditory cortex (right side of figure).

Somatic Cortex Injection



GALAGO 1529 L

Auditory Cortex Injection



GALAGO 1495 R

after injections in the auditory field.

Thus, it would appear that all three sensory systems project descending axons to the deep layers of the tectum and that the target of each cortical field appears to be distinct. This, of course, does not preclude the possibility of convergence at the single cell level since the dendritic network of neurons in the deeper layers is quite extensive (Sprague, '75).

Having shown that the retrograde and anterograde transport methods lead to the same conclusions regarding the organization of the cortical projections onto the superior colliculus, it becomes an easy task to compare our results with those obtained using degeneration methods. Among the earliest anterograde degeneration studies to demonstrate a cortical projection to the superior colliculus were those of Mettler ('35, '36) using the Marchi method. Degeneration in the superior colliculus was noted following destruction of the temporal and parietal lobes in monkey. Using a refined silver technique, Whitlock and Nauta ('56) were among the first to describe terminal degeneration in the superior colliculus following removal of the temporal lobe in the monkey.

More recently, several studies have emphasized the laminar distribution of cortical terminals in the superior colliculus. In the monkey, Kuypers and Lawrence ('67) have described the organization of the projections of the neocortex onto the brain stem. The results show that there is a well-ordered arrangement in the terminations of corticotectal

pathways such that the various cortical areas--occipital, temporal, parietal, and arcuate--terminate at increasingly deeper levels of the superior colliculus. Thus, the occipito-temporal areas project to the superficial layers while the non-visual areas project onto the deeper layers.

In the cat, Garey et al. ('68) proposed that the visual, somatic, and auditory cortical fields send fibers to the superior colliculus and that these descending projections terminate in essentially the same manner as the corresponding ascending sensory pathways from the periphery. For example, the visual areas (17 and 18) project heavily onto the superficial grey lamina overlapping the projection from the retina. After destruction of the somatic cortex, degeneration is especially located in the posterior and lateral portions of stratum intermediale and stratum profundum overlapping ascending somatic sensory paths, especially the spinal tectal path (Antonetty and Webster, '75). Finally, the auditory cortex was shown to be especially connected with the caudal portion of the deeper layers.

Finally, a recent study in the tree shrew (Casseday et al., submitted) describes descending cortical projections using the retrograde transport of HRP. The results from this report indicate that each sensory field is especially connected with different portions of the tectum. Thus, area 17 projects to the superficial grey laminae while the visual belt projects to the rostral portion of stratum intermediale.

The somatic koniocortex was shown to have an exclusive target in the lateral portion of stratum intermediale while the projections of the somatic and auditory belts overlap in the caudal portion of the deeper layers.

To summarize, our results support the organization of corticotectal projections as revealed by anterograde and retrograde tracing techniques. First, the results support the notion that visual projections terminate more superficially than do projections from nonvisual areas. Second, our results indicate that the deeper layers are subdivided into regions each of which is connected with a particular sensory field. Third, brain stem nuclei containing labeled cells are functionally related to the cortical field containing labeled cells.

We have noted several species differences with regard to the laminar distribution of corticotectal projections. First, in the cat the projections of areas 17, 18, and 19 are essentially identical, in that each area sends a focal projection to the superficial layers and a nonspecific projection to the deeper layers (Kawamura et al., '74; Updyke, '77). Our evidence in Galago suggests that each of these visual areas project in an essentially non-overlapping manner onto the superficial layers, and we have no evidence that these areas project to the deeper layers. Second, in the tree shrew (Casseday et al., submitted; Harting and Noback, '71) only area 17 projects to the superficial grey while, in Galago, both areas 17 and 18 terminate in these layers.

The terminal distribution of corticotectal inputs is in close agreement with previous physiological evidence. Studies in the cat (Gordon, '73), mouse (Drager and Hubel, '75), and tree shrew (Albano et al., '78) support the laminar separation of visual and nonvisual inputs, demonstrating that in the upper layers (SZ and SG) the predominant cell type responds best to objects moved slowly across the receptive field. Drager and Hubel ('75) noted that somatic and auditory responses were most commonly found in penetrations underlying the representation of the temporal visual field. Bimodal and trimodal cells were found at the borders of transition between the visual and nonvisual layers and between clusters of somatic and auditory neurons, suggesting that multimodal convergence occurs only to a limited degree (Drager and Hubel). We would predict, from the relatively large number of corticotectal cells, that the influence of the cortex, especially auditory, on the receptive field properties of neurons in the superior colliculus would be profound. Apparently, this is not the case. In the cat (Stein, '78), cortical influence is critical in determining the response properties of visual neurons, but not in determining the responses of auditory and somatic neurons. The significance of this finding remains obscure.

Reciprocity of Connections

Another issue of some significance concerns the precision of reciprocal projections between the cortex and the pulvinar. This is an important issue inasmuch as it is a common finding in the somatic

(Jones and Powell, '68, '69) and auditory (Fitzpatrick et al., '77, '78) sensory systems and because it has been shown that the cortex has a profound influence on the activity of thalamic neurons (Kalil and Chase, '70). We have attempted to resolve this issue in two ways. First, we have examined the patterns of projections in the pulvinar complex following HRP and tritiated amino acid injections placed in the cortex. Second, we have compared the distribution of labeled cells in the cortex following HRP injections in the pulvinar with the distribution of cortical degeneration following lesions placed in the pulvinar. Suffice it to say that there appears to be precise, reciprocally organized interconnections between each cortical subdivision and its thalamic target. This finding is yet another way in which the unity of the pulvinar can be demonstrated.

Sensory Cortex

Traditionally, the cortex intercalated between area 17 and the auditory field has been considered association cortex (Diamond, '78). This definition was retained even after it was discovered that the pulvinar nucleus projects to much of the association areas (Walker, '38; Clark and Northfield, '37; Chow, '50); there was no known sensory projection to the pulvinar. Since then, the superior colliculus has been shown to project to at least portions of the pulvinar in a variety of mammals. In the tree shrew (Harting et al., '73b), for example, the entire pulvinar is the target of fibers from the superficial layers of the superior colliculus. In squirrel (Robson and Hall, '77), bushbaby (Glendenning et al.,

'75), and higher primates (Benevento and Fallon, '75), it had been shown with anterograde tracing methods that only the caudal portion of the pulvinar is a target of the tectal projections. Thus, it was argued that truly intrinsic subdivisions of the pulvinar evolved with the origin of primates and other mammalian lines.

These experiments alter that conclusion. We have shown that the entire pulvinar nucleus of Galago is the recipient of ascending sensory fibers and that it is a sensory relay nucleus. Furthermore, this finding suggests that the entire extrastriate cortex is primary sensory cortex.

Descending Projections: Significance of Layers V and VI

With regard to the layer of origin of descending corticothalamic projections, previous evidence has suggested the general proposition that layer VI projects to the thalamus and layer V projects to the tectum (Gilbert and Kelly, '75; Hollander, '74). But now we must qualify this generalization inasmuch as layer V of the striate cortex projects to the pulvinar nucleus. When the cells which are labeled after pulvinar injections--their size, number and distribution--are compared with the cells labeled in layer V after superior colliculus injections, it would seem likely that it is the same population of cells which is being labeled after each injection. In other words, this comparison suggests that the projections of area 17 to the pulvinar complex may consist of collaterals of

the axons which project to the superior colliculus. In any case, the descending projections provide further opportunities for parallel visual pathways to interact, and for the striate cortex to influence the various centers which relay impulses in the parallel tectopulvinar path.

ABBREVIATIONS

Ak or Aud kon, auditory koniocortex
Allo, allocortex
Am or Aud med, auditory medial cortex
AM, anterior medial nucleus
Ap or Aud post, auditory posterior cortex
Av or Aud vent, auditory ventral cortex
AV, anterior ventral nucleus
BC, brachium conjunctivum
BP, brachium pontis
C, caudate nucleus
CC, corpus callosum
CG, central gray
CIN, central intralaminar nucleus
Cing, cingulate cortex
CL, central lateral nucleus
CM, central medial nucleus
CN, cochlear nucleus
CP, cerebral peduncle
CUN, cuniform nucleus
d, dorsal division of the medial geniculate body
DNLL, dorsal nucleus of the lateral lemniscus
DVN, dorsal vestibular nucleus
ex, external nucleus of the inferior colliculus
FF, fields of Forel
GL, dorsal lateral geniculate body
GM, medial geniculate body
GM v or v, ventral division of the medial geniculate body
GTF, gigantocellular tegmental field
Ha, habenula nucleus

IC, inferior colliculus

ICc, central nucleus of the inferior colliculus

I-m, medial subdivision of the inferior pulvinar nucleus

Int, intralaminar nucleus

IO, inferior olivary complex

IP, interpeduncular nucleus

Lat, lateral nucleus

Lim, limitans nucleus

LL, lateral lemniscus

LOT, lateral olfactory tract

LSGS, lower stratum griseum superficiale

LVN, lateral vestibular nucleus

M4 or Mot 4, motor 4 cortex

Mb or M belt, motor belt cortex

mc, magnocellular division of the medial geniculate body

MD, mediodorsal nucleus

MRF, mesencephalic reticular formation

MSO, medial superior olivary nucleus

MTF, magnocellular tegmental field

NTB, nucleus of the trapezoid body

OB, olfactory bulb

Pb or Pbg, parabigeminal nucleus

PC, posterior commissure

peri, pericentral nucleus of the inferior colliculus

periarchi, periarchicortex

peripaleo, peripaleocortex

Ph, nucleus praepositus hypoglossi

Po, posterior group

Po a, anterior sector of the posterior group

Pp or parietal post, parietal posterior cortex

Proiso, proisocortex
Pt, pretectum nucleus
Pul I, inferior pulvinar nucleus
Pul S, superior pulvinar nucleus
Pv, periventricular nucleus
Py, pyramidal tract
Re, reuniens nucleus
Ret, reticular nucleus
Rh, rhomboidal nucleus
SG, superficial gray layers of the superior colliculus
Sg, suprageniculate nucleus
SI, stratum intermediale
Sk or Som kon, somatic koniocortex
S-M or Sens-mot, sensory motor cortex
SO, stratum opticum
SP, stratum profundum
SS belt, somatic belt cortex
Sub thal, subthalamus
Ta or Temp ant, temporal anterior cortex
Tm or Temp mid, temporal middle cortex
Tp or Temp post, temporal posterior cortex
Tv or Temp vent, temporal ventral cortex
USGS, upper stratum griseum superficiale
VA, ventroanterior nucleus
VGL, ventral lateral geniculate body
VL, ventrolateral nucleus
VM, ventromedial nucleus
VP, ventroposterior nucleus
ZI, zona incerta
III, nucleus of the oculomotor nerve

I, II, III, IV, V, VI, layers of neocortex

17, area 17 or the striate cortex

18, area 18

19, area 19

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